



Effects of oil spills on Arctic pelagic ecosystems - Winter exposure and variations in sensitivity

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Spatial ecology of lacustrine fishes: ecological effects and applied aspects

PhD Thesis



Written by Joan Holst Hansen
Defended 16 March 2018

SPATIAL ECOLOGY OF LACUSTRINE FISHES: ECOLOGICAL EFFECTS AND APPLIED ASPECTS

PhD thesis

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January 2018

Technical University of Denmark

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TABLE OF CONTENTS

PREFACE AND ACKNOWLEDGEMENT	4
LIST OF MANUSCRIPTS	6
SUMMARY	7
OBJECTIVES	15
THESIS INTRODUCTION	16
1. LAKE ECOLOGY, EUTROPHICATION, AND STUDY ORGANISMS	16
1.1. Lake ecology.....	16
1.2. Eutrophication.....	19
1.3. Study organisms	20
1.3.1. Pike	20
1.3.2. Cyprinid fish; roach and bream.....	22
2. SPATIAL ECOLOGY OF LACUSTRINE FISH: EFFECTS ON ECOSYSTEMS.....	24
2.1. Spatial ecology of fish; an introduction.....	24
2.1.1. Movement	25
2.1.2. Dispersal	25
2.1.3. Migration	26
2.1.4. Nomadism	26
2.2. Ecological effects of seasonal migrating prey	27
2.3. Ecological effects of within and between lake movements.....	29
3. APPLIED ASPECTS OF SPATIAL ECOLOGY	33
3.1. Lake restoration and biomanipulation	33
3.1.1. Biomanipulation by fish removal	34
3.2. Cost effective biomanipulation.....	35
3.3. Implications of inter-lake movements of large bream on biomanipulation measures.....	38
4. METHODS	40
4.1. PIT telemetry	40
4.2. Stomach content analysis.....	43
4.3. Stable isotope analyses	44
4.4. Measurement of water turbidity.....	45
CONCLUSION.....	47

REFERENCES49

PAPER I..... 65

PAPER II 101

PAPER III 129

PAPER IV 149

PREFACE AND ACKNOWLEDGEMENT

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January 2018

Joan Holst Hansen

LIST OF MANUSCRIPTS

This thesis is based on the following list of manuscripts:

- I. **Hansen, J. H.**, Skov, C., Baktoft, H., Brönmark, C., Chapman, B. B., Hulthén, K., Hansson, L.-A., Nilsson, P. A., & Brodersen, J. Ecological consequences of animal migration: prey partial migration affects predator ecology and prey communities. Submitted to *Journal of Animal Ecology*. (*Current status: Rejected with encouragement to resubmit*)
- II. **Hansen, J. H.**, Brodersen, J., Baktoft, H., & Skov, C. Relationship between bream (*Abramis brama*) activity and water turbidity in a shallow lake under different season conditions. *Hydrobiologia*. In review.
- III. **Hansen, J. H.**, Brodersen, J., & Skov, C. Partial nomadism in large-bodied bream (*Abramis brama*). Manuscript.
- IV. Skov, C., **Hansen, J. H.**, Baktoft, H., Brodersen, J., Brönmark, C., Hansson, L.-A., Hulthén, K., Chapman, B. B., & Nilsson, P. A. Biomanipulating streams: a supplementary tool in lake restoration. *Hydrobiologia*. In review.

SUMMARY

This thesis investigates aspects of the spatial ecology of lacustrine fishes, i.e. how movement patterns and activity may inflict on lake ecosystem functioning and applied lake management issues.

The first paper (**paper I**) explores changes in predator-prey interactions caused by partial migratory prey fish on top-predators foraging ecology. Specifically, it was tested whether partial seasonal migration of certain prey species within the overall prey community affected the foraging ecology of a top-predator (pike, *Esox lucius*). Partial-migratory prey fish leave the lake and over-winter in connected streams and therefore could cause a reduction in available prey biomass in the lake resulting in changes to the foraging ecology of resident predators, such as pike. These predator-prey interactions were examined in replicated freshwater lake systems, four with- and four without opportunity for prey migration. Specifically, predator foraging mode and prey community structure in lakes where cyprinid prey fish perform seasonal partial migrations into connected streams were compared with lakes with no migratory opportunities for prey fish. Results showed clear seasonal bottom-up effects of prey migration on foraging ecology of pike. Diet size-structure and species composition of predators in lakes exposed to migrating prey vary during the winter season compared to pike predators not experiencing fluctuating prey biomass. Furthermore, pike exposed to migrating prey experience a size-specific change in littoral versus pelagic origin of diet, and reduced somatic condition during the prey migration period. In conclusion, seasonal prey migrations have important implications for predator foraging ecology, and may cause seasonal shifts in the importance of their supporting energy pathways.

In the second paper (**paper II**) the overarching theme was again to explore the link between spatial fish ecology and potential ecosystem effects through an examination of how the feeding activity of bream (*Abramis brama*), an important benthivorous fish in many lakes, may affect lake ecosystems including functionality. A potential relationship between benthivorous bream activity behavior and their impact on water turbidity was investigated on a day-to-day basis under natural conditions. Benthivorous bream are highly specialized ecosystem engineers with their foraging behavior disturbing the lake sediment in search of food organisms. This foraging behavior has several potential effects on the ecosystem, i.e. it results in resuspension of sediment, increasing water turbidity, prevents the establishment of submerged macrophytes through mechanic stress, and may cause release of nutrients retained in the sediments back into the water column. Bream foraging

behavior ultimately results in lower light penetration through the water column, loss of submerged macrophytes, decreases in zooplankton, and increases in phytoplankton in the lake. This study (the first full-scale under natural conditions) describes how bream activity influences lake turbidity on a day-to-day basis. A clear relationship between daily bream activity and water turbidity was found, particularly when water temperatures were relatively low (below 15°C). No clear relationship was found when water temperatures exceeded 15°C, likely due to effects being masked by the increased phytoplankton production during spring and summer. This finding adds an important seasonal dimension to the previous knowledge about the structuring role of benthivorous bream in lake systems, and implies that winter activity of benthivorous bream may play a role for maintaining lake ecosystems in a turbid state, e.g. by transferring nutrients from the benthic to pelagic realms, and potentially also by preventing important establishment of submerged macrophytes in the spring through shading or mechanical stress.

In the third paper (**paper III**), passive telemetry technology was used to describe long-term movement patterns of 1280 individually tagged adult benthivorous bream in a multi-lake drainage system during nine years. The movement patterns is best described as partial nomadism, where a part of the population are neither resident nor migratory but move between lakes in an unpredictable arrhythmic fashion, often with long residency in one lake before moving to the other lake. On average 15% of the tagged bream changed lake within the first year after tagging, but there was extensive variation in the amount of moving bream between years, from 0% to 37%. In total, 30% of the bream that changed lake returned to the lake of tagging after 1-3 years but the majority never returned. Notably, movements out of lakes were significantly more in direction of the neighboring lake than away from the sister-lake system, suggesting that at least direction was not random. This opens up for important questions regarding the mechanisms governing the patterns of nomadism. Further, since bream are important bioengineers, fluctuating densities of adult bream could cause instability in the ecological state of lakes.

The fourth and final paper (**paper IV**) focused on applied aspects of spatial ecology of lacustrine fish, i.e. how knowledge about seasonal movement patterns of cyprinid fishes can be used to improve current methods used to restore eutrophicated lakes. Specifically, the study explored how cyprinid fish removal from streams can be used as a tool in biomanipulation of lakes, i.e. as a supplement to the traditional in-lake fish removal. Cyprinid fish often perform seasonal partial migrations out of lakes and over-winter in streams. In Lake Søgård a small, eutrophic, shallow lake, results of two consecutive years demonstrated that it was possible to annually remove up to 35% of

the dominant cyprinid fish species via the stream. Further, it is argued that even higher amounts could be removed with a more targeted fishing effort, as up to 82% of the lake population moved into the streams during winter. These results indicate that fish removal from streams could be a supplementary tool in biomanipulation. Moreover, the method seems cost effective compared to other methods as seasonal migrating fish aggregate in fairly restricted areas within the stream and therefore are relatively easy to catch. When examining individual fish migration patterns in order to evaluate species- and length-specific variation in migration propensity, it was found that smaller planktivorous fish in general had a higher propensity to migrate compared to larger fish. Since large benthivorous fish, such as bream, do not participate in seasonal migration, fish removals from streams should be supplemented with in-lake removal methods in lake systems where benthivorous fish are the target group. As a rule of thumb, stream fishing seems most efficient when water temperatures are 2-6°C. Finally, prior to implementing fish removals from streams, it is argued that potential evolutionary consequences of the targeted removal of migratory phenotypes should be considered.

Combined, the results from this PhD thesis have provided new knowledge about spatial ecology of lacustrine fish in lakes, as well as knowledge about other aspects of the biology of these fish. For instance, how seasonal migration of cyprinid prey fish can influence fitness of a top predator as well as the energy pathways between trophic levels in lakes. The fact that this is showed in a replicated full scale ecosystem design, suggests robust results and the patterns found are likely to apply to, e.g. terrestrial ecosystems. Furthermore, the studies in this thesis provide new information about behavior of adult benthivorous bream. Bream activity within a lake was showed to influence water turbidity, even during cold periods of the year. Thereby, an important seasonal dimension was added to how adult bream can play a structuring role in eutrophic lakes. Likewise, the findings of unpredictable nomadic movements of adult bream between lakes add new information about the biology of adult bream. Moreover, these arrhythmic movement patterns can challenge previous practises, i.e. where lakes are managed as isolated units. Finally, since movements of adult bream between lakes are likely to result in fluctuating densities within a given lake, the findings in this thesis introduces a new explanation to why shallow eutrophic lakes sometimes alternate abruptly between different trophic states. Eutrophication is an important threat to many freshwater systems, such as shallow lakes, and biomanipulation is an important tool to mitigate this problem. Prospectively, findings of biomanipulation in streams as a cost effective supplementary tool to

traditional biomanipulation methods, can turn out to be valuable knowledge for future lake restoration projects.

DANSK RESUMÉ

Denne afhandling omhandler aspekter af den rumlige fordeling af søfisk samt de implikationer, deres bevægelsesmønstre og aktivitet kan have for forståelsen af søers økosystemer og forvaltning.

Den første artikel (**artikel I**) omhandler ændringer i den rumlige fordeling af byttedyr og deres påvirkning af rovfisk. Specifikt blev det testet, hvorvidt byttefisks sæsonmigration ud af søer påvirker fødeøkologien hos rovfisk (gedde). I lavvandede søer er det almindeligt, at en andel af byttefiskene migrerer (på engelsk ”partial migration”) ud af søen om efteråret og overvintrer i de tilhørende vandløb. Dette kan forventeligt medføre en nedgang i tilgængeligheden af bytte for gedden (som forbliver i søen) og dermed påvirke geddens fødeøkologi. Disse forhold blev undersøgt i et repliceret fuldskalaforsøgsstudie. Fødeøkologien hos gedder blev undersøgt hen over året i fire åbne søer, hvor byttefiskene havde mulighed for at migrere ud i vandløb, og sammenlignet med fødeøkologien hos gedder indsamlet i fire lukkede søer uden vandløb, hvor byttefiskene ingen mulighed havde for at migrere. Resultaterne viste, en sæsonmæssig påvirkning på geddens fødeøkologi forårsaget af byttefiskenes migration. Gedder i søer med migrerende bytte spiste således bytte af mindre størrelse og af en anden artssammensætning sammenlignet med gedder, som ikke oplevede svingende mængder af byttedyr i løbet af året. Endvidere blev det observeret, at ændringerne i fødevalg, alt efter geddernes størrelse, medførte en ændring i littoral versus pelagisk oprindelse af føden. Slutteligt viste resultaterne, at gedder sidst på vinteren, lige inden byttefiskene returnerede til søen fra vandløbene var i dårligere kondition end gedder i søer uden migrerende bytte. Samlet set er konklusionen, at sæsonvandring af byttefisk kan have konsekvenser for fødeøkologien hos rovfisk og formodentlig kan medføre sæsonændringer i energioprindelsen op gennem søens fødekæde.

Det overordnede tema i den anden artikel (**artikel II**) var ligeledes forbindelsen mellem fisks rumlige fordeling og potentielle påvirkninger på økosystemet. Mere præcist beskrives hvordan aktivitet af brasen, en vigtig fisk der primært lever af bunddyr i sedimentet, kan påvirke økosystemet i søer og herunder dens funktionalitet. Forholdet mellem aktivitetsniveauet hos brasen og vandets turbiditet (uklarhed), blev derfor undersøgt under naturlige forhold. Brasen, der lever af bundlevende dyr, er højt specialiserede ”økosystemingeniører”, som gennem deres fødesøgningsadfærd efter bundlevende fødeorganismer forstyrrer sedimentet i søen. Denne specifikke fødesøgningsadfærd kan resultere i, at bundmaterialet opslæmmes i vandet og dermed forårsager forøget turbiditet. Opslæmning af bundmaterialet kan desuden resultere i frigivelse af

næringsstoffer, ellers bundet i sedimentet, til vandsøjlen. Samlet set kan disse forhold føre til lavere lysindfald ned gennem vandsøjlen, dårlig vækst af undervandsplanter på grund af udskygning, reduktion af zooplankton og tilvækst af fytoplankton i søen. Endvidere kan den mekaniske stress af bundmaterialet, som brasens fødeaktivitet medfører, forhindre etablering af undervandsvegetation, hvilket kan bidrage yderligere til at søen fastholdes i den uklare tilstand. Resultaterne fra **artikel II**, som så vidt vides er det første studie, der har beskrevet hvordan brasenaktivitet påvirker vandets klarhed i søer på en dag-til-dag basis, viste en klar sammenhæng mellem daglig brasenaktivitet og vandets turbiditet, særligt når vandtemperaturen i søen var relativ lav (under 15 °C). Ingen klar sammenhæng mellem brasenaktivitet og vandets turbiditet blev fundet ved højere vandtemperatur (over 15 °C). Dette skyldes formodentlig, at den øgede fytoplanktonproduktion, som sker om foråret og sommeren, når vandet overstiger 15 °C, overskygger en given sammenhæng. Resultaterne følger en vigtig sæsonmæssig dimension til den nuværende viden indenfor området, idet brasenaktivitet i vinterhalvåret kan medvirke til, at fastholde søens økosystem i en uklar tilstand. Den uklare tilstand kan bibeholdes på grund af brasenaktivitet f.eks. som følge af frigivelse af næringsstoffer fra sedimentet til de frie vandmasser, ved at forhindre forårets etablering af undervandsplanter på grund af mekanisk stress eller fordi det opslæmmede bundmateriale i vandsøjlen skygger for deres vækst.

I den tredje artikel (**artikel III**) blev individuelle bevægelsesmønstre hos i alt 1280 bentivore brasen (brasen der lever af bundlevende dyr) undersøgt ved brug af telemetri i et vandsystem med søer og vandløb i ni år. En andel af de undersøgte brasen forblev i den samme sø gennem hele perioden, mens en anden bevægede sig rundt i vandsystemet i et nomade-agtigt mønster, dvs. i et uregelmæssigt og arytmsk vandringsmønster mellem søerne. Gennemsnitlig svømmede 15 % af de mærkede brasen til nabosøen indenfor det første år efter mærkningen. Der var dog stor variation mellem årene, idet tallet varierede fra 0 % til 37 %. 30 % af de brasen, der skiftede sø, vendte på et tidspunkt tilbage til den sø, de blev mærket i, men størstedelen vandrede ikke tilbage. Brasen bevægede sig primært mellem de to nabosøer og kun i mindre grad ud i vandløbene væk fra søerne, hvilket peger på at vandringsretningerne ikke var tilfældige. Resultaterne giver således ny viden om nomadeadfærden hos fisk. Derudover, fordi bentivore brasen er vigtige ”økosystem-ingenerer” i særligt lavvandede søer, kan en sådan nomadeadfærd resultere i fluktuerende bestandstætheder og dermed ustabilitet i søernes vandklarhed og økosystemets tilstand.

Den fjerde og sidste artikel (**artikel IV**) fokuserer på, hvordan viden om den rumlige fordeling hos søfisk kan anvendes i en praktisk forvaltningsmæssig sammenhæng. Det vil sige, hvordan viden om

fredfisks sæsonmigration mellem søer og vandløb kan forbedre mulighederne for at restaurere eutrofe lavvandede søer. Fredfisk, inklusiv familien af fisk der betegnes cyprinider, foretager ofte (også beskrevet i **artikel I**) sæsonmæssige migrationer mellem søen og tilhørende vandløb, hvorfor en større eller mindre andel af populationen opholder sig i vandløbene hen over vinterhalvåret. I studiet blev det undersøgt, om opfiskning af fredfisk fra vandløb i vinterhalvåret, kan bruges som en supplerende metode til de nuværende opfiskningsmetoder brugt ved biomanipulation. Undersøgelsen fandt sted i Søgård Sø, en forholdsvis lille, lavvandet og eutrof sø, hvor opfiskninger fra vandløb, ved hjælp af elektrofiskeri, foregik to vintre i træk. Resultaterne viste, at vandløbsopfiskninger årligt kunne fjerne op til 35 % af søens bestand af dominerende fredfiskearter. Eftersom op til 82 % af fredfiskene fra søen vandrede ud i vandløbet om vinteren, argumenteres det at det er muligt at fjerne en endnu højere andel fra vandløbet med en mere målrettet og effektiv fiskeindsats i vandløbet. Undersøgelsen peger derfor på, at det vil være muligt at benytte opfiskning i vandløb som et supplerende redskab til biomanipulation. Desuden er denne metode ikke så omkostningstung sammenlignet med andre opfiskningsmetoder (i søen), da de vintervandrede fisk ofte samles i et begrænset område i vandløbet og derfor kan være forholdsvis nemme af opfiske. For at undersøge om der var arter og størrelser af fisk, som vandrede mere end andre blev de individuelle fiskemigrationsmønstre undersøgt. Disse resultater viste, at især de mindre fisk, der ofte lever af zooplankton, generelt havde større tendens til at migrere end de større fisk (f.eks. store bentivore brasen). Da store bentivore fisk, som brasen, således ikke foretager denne sæsonmæssige migration, bør opfiskning i vandløbet suppleres med fjernelse af disse fisk i selve søen, især i de søer hvor fjernelse af bentivore fisk er en forudsætning for et succesfuld biomanipulationsprojekt. Opfiskning i vandløbet var mest effektiv når vandtemperaturen var mellem 2° C og 6 °C. Slutteligt skal det fremhæves, at inden opfiskning i vandløb implementeres som en generel metode i biomanipulation, er det vigtigt at overveje eventuelle evolutionære konsekvenser af en så målrettet fjernelse af migrerende fænotyper.

Samlet set har undersøgelserne i denne Ph.d. afhandling bidraget med ny viden om den rumlige fordeling af søfisk, samt de implikationer deres bevægelsesmønstre og aktivitet kan have for søers økosystemer, forvaltning og for fiskenes biologi. Et eksempel er, hvordan rovfisk som gedden bliver påvirket i søsystemer, hvor tætheden af byttefisk varierer over året på grund af byttefiskenes sæsonvandring. Resultaterne peger på, at dette ikke blot påvirker geddens fødeøkologi og ultimativt kropskondition, men der sker også et skifte i oprindelsen af energikilder (pelagisk versus

littoral). Dette blev demonstreret i et repliceret fuldskalastudie, og de robuste resultater antyder, at de fundne mønstre kan overføres til andre økosystemer (f.eks. terrestriske). Studierne i Ph.d.-afhandlingen præsenterer også vigtig ny viden om adfærden hos bentivore brasen. Det blev demonstreret, hvordan bentivore brasens aktivitet i en sø, påvirker søens turbiditet i årets kolde måneder og derved føjer en vigtig sæsonmæssig dimension til, hvordan og hvornår brasen kan have en strukturende rolle i søers økosystemer. Tilsvarende bidrager opdagelsen af, at en andel af brasenbestanden fra tid til anden kan vandre mellem søer med ny viden om brasens biologi. Det faktum, at disse søskift foregår i et tilsyneladende uforudsigeligt nomade-agtigt mønster, er ikke bare spændende ny viden, men kan samtidigt udfordre dele af den hidtidige forvaltning af søer, dvs. hvor søer forvaltes som isolerede enheder og ikke på vandsystems niveau. Når større eller mindre tætheder af brasen pludselig foretager skift mellem søer, vil det ultimativt påvirke tætheden af brasen i den enkelte sø. Eftersom tætheden af brasen kan være afgørende for søernes økologiske tilstand, bidrager disse undersøgelser med en ny forklaring på, hvorfor nogle lavvandede eutrofe søer indimellem brat skifter mellem at være i en klarvandet eller en uklar tilstand. Eutrofiering er en vigtig trussel for mange sø-systemer og søer, ikke mindst lavvandede søer, og her er sørestaurering via biomanipulation, et af de vigtigste virkemidler til en mulig løsning. Resultaterne angående opfiskning af søernes fredfisk fra vandløb om vinteren viser, at dette er et kosteffektivt supplement til eksisterende metoder, hvilket kan vise sig værdifuldt i fremtidige sørestaurerings-projekter.

OBJECTIVES

This thesis focused on spatial ecology of lacustrine fish and how they can affect lake ecosystem functioning. Furthermore, applied aspects of spatial ecology are explored e.g., how to utilize seasonal migration of cyprinids as a supplementary tool for biomanipulation of shallow eutrophic lakes. Spatial ecology in this thesis is defined as the ultimate distribution or spatial unit occupied by a species and its effects on individual species' dynamics and the structure, dynamics, diversity, and stability of multispecies communities (Tilman & Kareiva, 1997). Spatial ecology in this thesis covers a variety of movement types i.e. between lake and tributary movements (seasonal migration) (**paper I** and **IV**), within lake movements and activity (**paper II**), and between lake movements (nomadism; **paper III**). The specific objectives of the thesis are:

- To examine how partial migration of prey affects prey fish community structure as a consequence of species-specific ability to escape predation risk during winter, and resulting potential alterations of the relative dominance of the littoral and pelagic food chains in the energy flow from primary producers to top-predators (**paper I**).
- To increase knowledge about seasonal dynamics in bream activity and how it impacts water turbidity in shallow lakes under natural conditions (**paper II**).
- To describe movement of adult benthivorous bream between two shallow lakes using a time-series of nine contiguous years. More specifically, to explore seasonal and daily patterns as well as the magnitude of the movements, i.e. the percentage of the populations in the two lakes that move from one lake to the other. Furthermore, to explore return patterns, i.e. if and when bream return to the lake of first observation following a shift to another lake (**paper III**).
- To investigate if removing cyprinid fish from streams connected to their home lake during the winter migration period could be an efficient, complementary method to lake fishing in biomanipulation efforts. In detail, to quantify seasonal migration patterns of common cyprinids belonging to different functional groups, i.e. roach (*Rutilus rutilus*), common bream, and white bream (*Blicca bjoerkna*), and to perform fish reductions by electrofishing in a lake inlet stream during two consecutive years (**paper IV**).

The thesis opens with a general introduction that lays out the framework for the research, summarizes, and discusses the main findings in **papers I** to **IV** and close with **paper I, II, III, and IV**.

THESIS INTRODUCTION

This thesis explores spatial ecology of lacustrine fish, i.e. related to freshwater lakes, and how their movement and activity patterns may influence higher and lower trophic levels and lake ecosystem functioning. Furthermore, applied aspects are explored, such as how to utilize seasonal migration of cyprinids as a supplementary tool for biomanipulation of shallow eutrophic lakes. The thesis introduction is divided into four chapters. First chapter comprises a general introduction to lake ecology with special focuses on eutrophication and how it impacts interactions between functional groups as well as an introduction to the biology of pike, roach, and bream which are the main study organisms included in this thesis. In the second, chapter different components of spatial ecology are defined and discussed. Next, the importance of spatial ecology on lake ecosystem functioning is discussed in relation to the current thesis. The third chapter outlines the applied aspects of this work, mainly in relation to lake restoration of eutrophic lakes, including a thorough introduction to the concept of lake restoration and lake restoration by fish removal in particular. In chapter four, the main methods used in these studies are presented. Finally, the conclusions of the thesis studies are presented.

1. LAKE ECOLOGY, EUTROPHICATION, AND STUDY ORGANISMS

This section introduces lake ecology and includes a description of different habitats that exist within freshwater lakes and their associated species as well as a characterization of the biological linkages among habitats. Furthermore, this section includes a description of eutrophication's role for lake ecosystem functioning, a central topic in **papers II and IV**. The last section of this chapter includes the biology of the three main study organisms, pike, roach, and bream.

1.1. Lake ecology

A lake is a water body localized in a basin surrounded by land and the idea that lakes are isolated from the surrounding landscape goes back at least to the late 19th century (Forbes, 1887 (reprinted in 1925)). The concept of a lake as an isolated unit is still a central theme in research and management of freshwater systems and is a fundamental assumption of limnology (Magnuson et al., 1998; Daniels et al., 2008). However, lakes are often connected to inlet and/or outlet streams that serve to feed or drain it, and hence the viewpoint of a lake being an isolated ecosystem often

ignores the connectivity that exists among lakes, streams, and even landscapes (Magnuson & Kratz, 2000).

The majority of lakes throughout the world are small ($< 1 \text{ km}^2$ surface area) and shallow ($< 10 \text{ m}$ mean depth), as demonstrated in a global survey made by Wetzel (1990). Lakes are complex ecosystems composed of distinct habitats coupled by biological, physical, and chemical processes. A lake can typically be divided into three habitats as pelagic, littoral, and benthic habitats (Fig. 1). The pelagic habitat is the open-water components of the lake. Pelagic habitats are inhabited predominantly by planktonic organisms such as microscopic bacteria, viruses, protozoa, phytoplankton, zooplankton, as well as invertebrates and fishes (Schindler & Scheuerell, 2002). The physical and chemical structure of the pelagic habitat is relatively homogeneous in the horizontal dimension, but can have substantial vertical heterogeneity associated with thermal and chemical stratification (Schindler & Scheuerell, 2002). The littoral habitats are defined as nearshore, shallow areas where water depth is less than the compensation depth (Vanni, 1996). Compensation depth is the depth at which there is sufficient light for photosynthesis to balance respiration. Thus, sunlight can penetrate throughout the water column of littoral habitat, allowing macrophytes to grow.

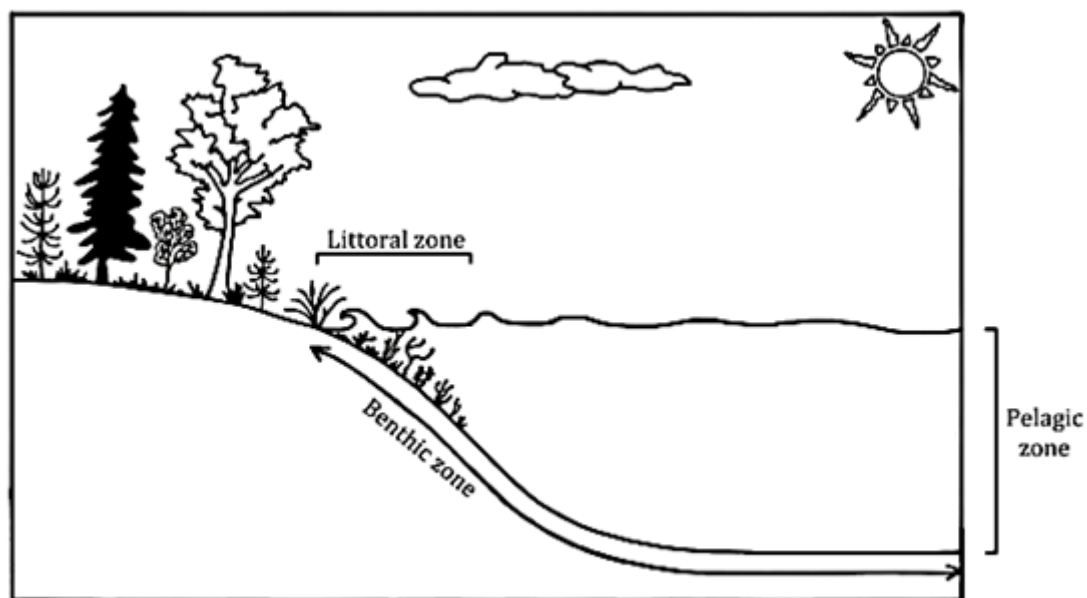


Figure 1: A cross-section of a lake illustrating the habitats that organisms inhabit (Modified from Koopal & Curtis, 2017).

Macrophytes, in addition to being food source and substrate for algae and invertebrates, provide a habitat that is different from the pelagic environment and can serve as camouflage and/or shelter for e.g. fish (Timms & Moss, 1984; Persson & Eklöv, 1995; Schriver et al., 1995). Furthermore, submerged macrophytes bind nutrients and stabilize the sediment reducing resuspension by wind (Donk & Bund, 2002; Nurminen & Horppila, 2009). The benthic habitats are the area associated with the bottom in lakes and can be considerably heterogeneous in both horizontal and vertical dimensions (Lodge et al., 1988). This heterogeneity is associated with a variety of sediments, rocks, and aquatic plants (Eschmeyer, 1936; Covich et al., 1999). The dominant taxa in benthic habitat are algae, bacteria, protozoa, aquatic insects and other invertebrates, and fishes (Schindler & Scheuerell, 2002). Even though lakes are divided in different habitats, this far from means that coupling between habitats and trophic interactions do not occur. For instance, nutrients flow via trophic interactions from primary producers to zooplankton grazers, to invertebrates and vertebrate zooplanktivores, and eventually to top predators (mainly fish; Schindler & Scheuerell, 2002). The typical Danish lake is shallow (Kristensen et al., 1990) and differ from deep lakes in several respects. Deep lakes are often thermally stratified during the summer, with poor exchange of nutrients and oxygen between the photic zone (surface layer that receives sunlight) and the lake bottom compared with shallow lakes that are typically homothermal (Imboden & Wüest, 1995; Jeppesen et al., 1997). Moreover, shallow lakes imply higher sedimentation and higher nutrient release from the sediment. The sediment of shallow lakes is, therefore, more important to nutrient turnover and trophic dynamics than in deep lakes, hence the benthic-pelagic coupling is stronger (Scheffer, 2004). Furthermore, a larger part of the lake area and volume may be covered by submerged macrophytes in shallow lakes, which as mentioned above, have proved to be of regulatory importance for lake ecosystems (Jeppesen et al., 1997).

Freshwater ecosystems, as all ecosystems, are exposed to gradual changes in nutrient loading, habitat fragmentation, biotic exploitation, or climate. Ecosystems are usually assumed to respond to such gradual changes in a steady way. However, studies have shown that steady change can be interrupted by sudden drastic nonlinear changes to a contrasting state (Scheffer et al., 2001). This led to the theory of alternative stable states where ecosystems can exist under multiple states and shifts between states are abrupt, rather than gradual. In particular, two alternative stable states exist for shallow lakes over a range of nutrients concentrations. One state comprises of clear water dominated by submerged macrophytes (oligotrophic) and the other of turbid water dominated by phytoplankton (eutrophic) (Scheffer et al., 1993; Scheffer & Carpenter, 2003; Williams, 2005).

Each of these stable states has a number of buffering systems that maintain the dominance of the particular state through top-down and bottom-up processes. Attempts can be made to influence these processes and thus force a change from one state to another, which is especially true during lake restoration projects when it can be desirable to convert a turbid lake into a clear water lake (Williams, 2005).

1.2. Eutrophication

Eutrophication, (the motivation for **papers II and IV**), has been, and continues to be, an important threat to lakes, especially for lakes located close to urban and agriculture areas (Brönmark & Hansson, 2002). Eutrophication is the enrichment of aquatic systems by nutrients, typically compounds containing phosphorus, nitrogen or both (Schindler, 1977). Eutrophication has strong impacts on lake ecology as it leads to structural changes to the ecosystem such as: increased production of phytoplankton and algae, higher biomass of zooplanktivorous and benthivorous fish species, general deterioration of water quality, etc. (Jeppesen et al., 2000; Søndergaard et al., 2007). Eutrophication occurs most often as a result of human activity (Edmondson, 1972; Coveney et al., 2005; Yang et al., 2008). Many lakes located in densely populated or near intensively agricultured areas have become eutrophic and thus turbid (Edmondson, 1972; Coveney et al., 2005; Yang et al., 2008) as a consequence of fertilization by humans. An excessive discharge of phosphorus and sometimes also nitrogen causes ideal conditions for phytoplankton production resulting in turbid water and decreased biological diversity (Jeppesen et al., 2000; Søndergaard et al., 2007). Consequently, algal blooms limit light penetration through the water column, reducing growth and potentially inhibiting submerged macrophytes as well as potentially reducing the foraging success (and biomass) of visual predators, including piscivores fish (Lehtiniemi et al., 2005; Persson et al., 1988; Jeppesen et al., 1990). Furthermore, high rates of photosynthesis related to eutrophication can deplete dissolved inorganic carbon in the water column and, during daylight, raise the pH of the water. Increased pH can have fatal consequences for organisms such as gastropods whose chemosensory abilities rely on perception of dissolved chemical cues (Turner & Chislock, 2010). When these dense algal blooms eventually die, microbial decomposition severely depletes dissolved oxygen, creating hypoxic or anoxic zones with lethal consequences for organisms unable to avoid such areas. Additionally, zooplanktivorous and benthivorous fish biomass and density increase with increasing nutrient load and especially with increasing total phosphorus concentration (Hanson & Leggett, 1982). This result in increased predation pressure on zooplankton and thus, decreasing

grazing pressure on phytoplankton. Furthermore, benthivorous fish disturb the lake sediment when searching for food which can increase and/or maintain eutrophication processes especially in shallow lakes (Box 1).

Eutrophication is a severe problem in Europe, including Denmark where the majority of lakes are situated near urban areas and cultivated land resulting in excessive nitrogen and phosphorus loading leading to observations of high phytoplankton production, turbid water, and decreased biological diversity (Jeppesen et al., 2000; Søndergaard et al., 2007). Submerged macrophytes have either been reduced severely or disappeared completely in most Danish lakes, and the fish assemblage has changed with a reduction of predatory fish species such as perch (*Perca fluviatilis*) and pike, and an increased dominance by zooplanktivorous and benthivorous fish such as roach and bream (Jeppesen et al., 1999). In Denmark, nutrient pollution accelerated in the 1960s before sewage treatments were established in urban areas (Jeppesen et al., 1998), and it is still a major problem for many Danish lakes. Various initiatives have been implemented through the past decades in order to restore the water quality in eutrophic lake systems (described further in chapter 3.1).

1.3. Study organisms

The three primary fish species of interest throughout this thesis are pike, roach, and bream. These are all lacustrine, although they can also be stream dwelling and sometimes even move into saline areas (Mills, 1991; Vehanen et al., 2006; Kottelat & Freyhof, 2007). This section, gives a short introduction to these three species and briefly highlight where this thesis have provided new information about the biology of these fish. Further discussion of ecological and applied aspects will follow in chapters 2 and 3.

1.3.1. Pike

Pike is an iteroparous, large-bodied (up to 130 cm) and long-lived (up to 30 years) fish species that exist in oligotrophic, mesotrophic, and eutrophic lakes (Muus & Dahlström, 1981; Larsson et al., 2015). Pike have a wide distribution area and are naturally found in fresh water lakes throughout the northern hemisphere, including Europe, North America, and Russia (Craig, 1996). However, they also occupy rivers (Vehanen et al., 2006; Hodder et al., 2007) and brackish waters, such as the Baltic Sea where the salinity is low (e.g., Westin & Limburg, 2002; Rothla et al., 2012). Pike is commercially very valuable and an important fish species for recreational and commercial fishing (Arlinghaus & Mehner, 2004; Lehtonen et al., 2009) and consequently has also been introduced and

stocked to areas both within and outside of its native range (McMahon & Bennett, 1996; Reynolds, 2011). Young pike are planktivorous fish, however it is essential for such young pike to optimize their foraging and undergo ontogenetic transition from planktivory to piscivory, and simultaneously minimize the risk of size-dependent cannibalism and predation (Bry, 1995). Larger pike are typically ambush predators performing sit-and-wait hunting behavior (Webb & Skadsen, 1980; Casselman & Lewis, 1996), mainly using vision to detect prey (Casselman, 1996). Therefore, pike feeding rate can be negatively affected with reduced visibility conditions (Craig & Babaluk, 1989; Jönsson et al., 2013). However, pike can use alternative sensory modes such as the lateral line (Raab, 1988; Nilsson & Eklöv, 2017) which may, to some extent, compensate for reduced visibility due to, e.g. turbid water. Furthermore, some previous studies have demonstrated that pike feeding rate are not limited by low water visibility if prey availability is relatively high (Skov et al., 2007; Nilsson et al., 2009).

Vegetation is an important part of pike habitat, especially for spawning and nursery areas (Bry, 1996). Vegetation acts as cover from predation and cannibalism and can provide a habitat for pike to hide in waiting for passing prey fish (Craig, 1996). While small pike are usually associated with vegetation, larger individuals more frequently inhabit a vegetation-open water interface or less-vegetated areas (Grimm & Backx, 1990; Casselman & Lewis, 1996). Also the importance of vegetation for pike foraging in turbid water is decreased; here pike sometimes occupy open water that provides corresponding high foraging success (Skov et al., 2003; Andersen et al., 2008). Most studies on pike activity describe high individual variability in activity level (e.g. Diana et al., 1977; Kobler et al., 2009; Baktoft et al., 2012). Adult pike often exhibit one of two different activity strategies, with some occupying small vs. large ranges (Jepsen et al., 2001; Vehanen et al., 2006). Pike is a keystone predator that can exert top-down effects on a fish community, shaping composition as well as abundance and distribution of their prey (Craig, 1996). However, as demonstrated in **paper I**, the feeding biology of pike can also be affected by bottom up processes. In this study, a replicated full-scale lake is used to demonstrate that inlets and outlets represent predator refuges for prey species to escape predation risk from pike, i.e. by performing seasonal migration out of the lakes and into the tributaries. Hence, during winter, when this prey migration takes place, pike can experience impaired food availability resulting in periods where somatic condition is reduced.

1.3.2. Cyprinid fish; roach and bream

Roach and bream both belong to the family of Cyprinidae, a large family, including over 2,400 species of freshwater fish that comprise the carps and true minnows (Eschmeyer & Fong, 2015). Roach and bream exist in various environments such as freshwater lakes, slow-moving rivers and streams, and in brackish waters. Roach and bream are highly common throughout western Eurasia (Kottelat & Freyhof, 2007). Roach and bream are iteroparous fish with reproductive seasons occurring during spring. However, roach usually spawn slightly earlier than bream, specifically from March to June while bream usually spawn from April to June (Poncin et al., 1996). Roach and bream are trophic generalists, employing a broad trophic niche, and utilize resources ranging from detritus (Persson, 1983a) and cyanobacteria (Kamjunke et al., 2002) to zooplankton (Lammens, 1985; Haertel & Eckmann, 2002), macrophytes, and benthic macroinvertebrates (Lammens & Hoogenboezem, 1991; Persson & Hansson, 1999). Adult roach typically shift to pelagic prey in the presence of specialist benthivorous (Persson, 1983b; Bergman & Greenberg, 1994) while adult bream typically undergo ontogenetic shifts in diet, from feeding on zooplankton in pelagic habitats to feeding on benthic invertebrates buried in the sediment (i.e. shifting to specialized benthivorous; Persson & Brönmark, 2002). Bream has a laterally flattened and high-backed body shape and a slightly undershot mouth, which it can extend as a feeding tube while searching for food items in the sediment. As presented in Box 1, the benthivorous feeding of adult bream can have detrimental impacts on lake ecosystems. In **paper II**, this idea is explored seasonally, demonstrating that sediment disturbance in a shallow lake can also take place during winter, i.e. there was a clear relationship between daily bream activity measured by telemetry and water turbidity at water temperatures < 15°C.

Relatively little is known about the spatial ecology of roach and bream. However, bream from the brackish estuaries of the Black, Caspian, and Azov Seas have been observed performing large seasonal migrations of up to 100 km during spring and autumn between spawning and winter grounds (Backiel & Zawisza, 1968). Former studies have also demonstrated upstream-downstream movements for both roach and bream in river systems (L'Abée-Lund & Vøllestad, 1985; Mills, 1991; Molls, 1999). The spring time spawning migration in rivers occurs in April to July and can vary from a few km to up to 60 km (Molls, 1999; Lucas & Baras, 2001; Lilja et al., 2003).

During the last 10-15 years, several studies have demonstrated that both roach and bream perform seasonal partial migration in shallow lakes (e.g., Brodersen et al., 2008a; Skov et al., 2008), with

some fish leaving lakes to connected streams during early autumn and overwinter in streams before returning to the lake in the spring, whereas other individuals remain lake residents all year round (Jepsen & Berg, 2002; Skov et al., 2008). This behavior is further confirmed in **papers I and IV**. One reason for cyprinid fish to perform this seasonal partial migration behavior is a trade-off between predation risk and growth rate (Brönmark et al., 2008). Cyprinid fish overwinter in streams where food availabilities and growth opportunities are less compared to the lake, however the stream wintering grounds hold low densities of stationary piscivorous predators and hence the predation risk is lower (Brönmark et al., 2008). Therefore, cyprinid partial migration is most likely regulated by seasonal- and habitat-specific changes to growth-mortality trade-offs. Seasonal partial migration from the lake and into streams is not observed in deep lakes. Instead, cyprinids often aggregate in deep water during the winter season (Bohl, 1980; Pavlov et al., 1986). Large bream do not perform seasonal partial migration as described above, probably because large bream are not at high risk of being preyed upon within the lake, simply because of their large body size. When bream physically outgrow their predators (primarily pike) gape size, the risk of predation is reduced substantial, i.e. they grow into a size refuge. This was demonstrated by a previous study in one of the study lakes used in the current thesis (Lake Loldrup) where Skov et al. (2011) showed that whether an individual bream migrated out of the shallow lake and into the connected streams could be predicted by its size-dependent predation vulnerability. Individuals with a low vulnerability of predation risk also had a low probability of migration. Consequently, the predation vulnerability of bream and hence its probability of migration is specific to the composition of predators and their gape size in the lake they inhabited (Skov et al., 2011). In line with this, the combined results from **papers III and IV** highlight that spatial ecology of bream change with ontogeny from seasonal migration between lake and tributaries in younger individuals (Skov et al., 2011, **paper IV**) to more random and unpredictable movement patterns between neighboring water bodies in large adults, i.e. movement patterns proposed here as partial nomadism.

2. SPATIAL ECOLOGY OF LACUSTRINE FISH: EFFECTS ON ECOSYSTEMS

This chapter presents a general introduction to spatial ecology of fish, including different categories of movement behavior. Followed by the main results found in **paper I, II, and III** about spatial ecology of lacustrine fish, i.e. the impacts that spatial ecology of bream, roach, and pike can have on ecosystem functioning.

2.1. Spatial ecology of fish; an introduction

Animal movement is an adaptation to spatiotemporal fluctuating resources, either seasonally or more unpredictably (Dingle & Drake, 2007), and the reasons for this spatial relocation and change in their environment are multiple, however, the overall goal is to increase fitness. The definition of spatial ecology, used in this thesis, is the ultimate distribution or spatial unit occupied by a species and its effects on individual species' dynamics and the structure, dynamics, diversity, and stability of multispecies communities (Tilman & Kareiva, 1997). Fish spatial ecology determines a fish's access to resources such as food, shelter, and potential mates as well as vulnerability to potential threats including predators. Spatial ecological resolutions of freshwater fish range from small-scale, lightning burst movements, for ambushing prey or escaping predators, to large-scale movements that covers several, even thousands, of kilometers up and down rivers (Koehn & Crook, 2013). The patterns of movement reflect the diversity of behavior, physiology, trophic interactions, and life history strategies. In nature, where a specific habitat is shared by several species, each species is usually restricted to its own spatial niche since two or more species in the same general habitat cannot usually occupy the same ecological niche for any significant length of time (Ayala, 1970). Hence, movement is one of the main options available to fish when responding to changes in their environment including species interactions. Thus, the variation in spatial ecology is often caused by certain interactions within and between species, such as competition for resources, reproduction, and predation (Lucas & Baras, 2001). Because fish are important organisms in freshwater ecosystems, knowledge of spatial movements from one habitat to another is important for a holistic understanding of ecosystems, since it could potentially have profound impacts upon ecosystem dynamics (Brodersen et al., 2008b; Post et al., 2008; Brönmark et al., 2010). As examples, spatial movement of fish could impact their surrounding environment through redistribution of energy and nutrients (Vanni, 2002; Koyama et al., 2005; Schindler et al., 2005), food-chain effects such as

trophic cascades (Fryxell & Sinclair, 1988; Brodersen et al., 2008b), and eco-evolutionary effects (Brönmark, et al., 2014).

Migration, movement, and/or dispersal occur in all groups in aquatic ecosystems, e.g. fish, birds, insects, and plankton, at some point during their life history to a lesser or greater degree. The different strategies of movement most likely have evolved because they affect individual survivorship. Animals leave habitats where resources are becoming scarce to colonize or take refuge in habitats where resources are available. More precisely, animals may leave habitats for very specific needs which either can be for favorable environments for reproduction, richer food resources, searching for better environmental conditions in terms of habitat or space (i.e. overpopulation and competition), or favorable climatic conditions during specific life stages. On the other hand it might also be to avoid predators, parasites, diseases, or other factors of stress.

Spatial ecology of lacustrine fish species is associated with different categories of movement behavior. The following section defines terms used throughout this thesis: movement, dispersal, migration, and related to the latter two, nomadism.

2.1.1. Movement

Fish movement may not be a clear directional movement behavior. It refers to populations (or part of populations) or individuals that change location at any temporal or spatial scale (Koehn & Crook, 2013). Hence, the term movement is used when not referring to specific kinds of locomotion (i.e. migration and dispersal) and includes all other ways of displacement.

Movement per time unit, i.e. activity, is a central theme in **paper II**.

2.1.2. Dispersal

Dispersal of fish represents the repositioning of fish, actively or passively, from their natal habitat in the search of fitness gain. Additionally, dispersal is movement of fish populations (or part of populations) or individuals from areas where they are concentrated to new areas where they are less concentrated (Koehn & Crook, 2013; Hansson & Åkesson, 2014).

2.1.3. Migration

For most people the word migration calls forth visions of spectacular seasonal movements of whole animal populations over long geographical distances. What can be classified as migration has been debated and several definitions are found in the literature (Baker, 1978; Dingle & Drake, 2007; Brönmark et al., 2014). However, this thesis takes a rather broad definition of migration in accordance with Hansson & Åkesson, 2014: Fish migration occurs when populations (or parts of populations) move between two well-defined habitats on a temporally (reasonably) predictable basis. Hence, fish migration is a cyclic process, and takes place at regular intervals of time, e.g. annual or seasonal in connection with life history traits.

A special type of migration, partial migration, is central to **papers I, III, and IV** (see also chapter 1.3.2). Partial migration, a prevalent form of migration, occurs when a population contains both migratory and resident individuals (Chapman et al., 2012). Partial migration has long been documented amongst salmonid fish species, where a part of the population migrates from freshwater to sea (anadromy) and others remain resident in their natal streams (Jonsson & Jonsson, 1993). Partial migration is however an extremely widespread phenomenon amongst fish species, not only anadromous but also catadromous (spawn in marine habitats and migrate to freshwater as juveniles and adults), potadromous (migration between freshwater habitats), and oceanodromous (migration between marine habitats) fish (Chapman et al., 2012).

2.1.4. Nomadism

Whereas dispersal and migration are general terms to describe movement, nomadism can be considered as a specific movement pattern (Holyoak et al., 2008) including elements from both dispersal and migration terminology. Examples of nomadism generally concerns mammals (e.g. Fryxell et al., 2004; Singh et al., 2012) or birds (e.g. Andersson, 1980; Korpimäki et al., 1987; Allen & Saunders, 2002), whereas nomadism in fish has been suggested (e.g. Myers, 1949; Quinn & Brodeur, 1991), but rarely described in larger detail. The mechanisms behind nomadism seem understudied and nomadism has had various definitions. However, most definitions include that the movement patterns of nomads are unpredictable in time and space (Mueller & Fagan, 2008). Nomadism also implies that individuals may sometimes move in large numbers (Jonzén et al., 2011).

Paper III proposes that movement patterns of adult bream between two neighboring lakes fits the description of nomadism. During a nine years study period, passive telemetry (see section 4.1 for an introduction to this) was used to explore between lake movements and found they were indeed arrhythmic and unpredictable in time, i.e. illustrated by a strong annual variation in the proportion of between lake movers, and in space, i.e. some individuals travelled between lakes more than once. Interestingly, not all of the bream populations, in either of the two lakes, participated in the between lake movements, i.e. some individuals were resident. Hence we argue that the nomadism was partial. Nomadism is thought to occur when resources fluctuate irregularly on a multi-year timeframe (Mueller & Fagan, 2008) and since resources also could relate to available spawning sites, observed nomadism in this study is discussed in association with availability of suitable spawning grounds.

2.2. Ecological effects of seasonal migrating prey

When animals move from one ecosystem to another, it is inevitable that they deposit nutrients and energy into the new ecosystem (Bauer & Hoyer, 2014). This transfer of resources (excreta, reproductive material, or the dead bodies of the relocated animals themselves) represents a loss of energy and nutrients (Milner-Gulland et al., 2011) from the origin ecosystem and a source to the destination ecosystem. Because of the potential for massive animal aggregation, e.g. as a result of migration or nomadism, during certain periods, the increased input of nutrients and energy can be substantial enough to drive the transition between alternative stable states (Holtgrieve & Schindler, 2011; section 1.1). Relocation of animals may affect both the ecosystem they travel to but also the one they leave. Relocation of animals can for example have profound ecological consequences through changes in predator-prey interactions (Post et al., 2008; Brodersen et al., 2011; **paper I**). Earlier studies have mainly focused on how resident predators respond to prey species relocating into the predator's home range and thus causing a temporary wealth of food opportunities for the predators (Hilderbrand et al., 1996; Samelius et al., 2011; Bauer & Hoyer, 2014). In contrast, much less attention has been paid to the counter scenario and the consequences for predators when they lose potential foraging opportunities, i.e. when their prey leaves the habitat. This is the focus of **paper I**, i.e. how the foraging ecology of top-predators is affected when a large percentage of their prey is leaving the ecosystem for a substantial part of the year. This was investigated using pike as a predator model species, comparing pike foraging ecology in lake ecosystems where a) their primary prey species (cyprinid fish species) perform partial migration and leave the lake to aggregate in the

connected streams during the winter season (further described in section 1.3.2 and 2.1.2) and b) lake ecosystems without connected streams and where horizontal seasonal prey migration therefore was impossible. Since pike do not follow their prey into the streams (e.g. Skov et al., 2011; **paper I**), it was hypothesized that pike in lakes where prey migrated would experience reduced foraging success (and possibly starvation) and/or alter their foraging strategies during migration periods. This hypothesis was explored via a replicated full scale design consisting of four freshwater lakes where prey fish have the opportunity to migrate and four lakes without the opportunity for prey fish to migrate. The study period proceeded from August 2011 to May 2012 and included the use of various methods including analysis of prey availability in all eight lakes, analyses of pike stomach content including estimations of prey biomass and size of ingested prey items. In addition, stable carbon isotope of white muscle tissue from pike was analyzed in order to study potential shifts in energy pathways associated with the experiment (see section 4.3). The results of **paper I** demonstrated clear seasonal bottom-up effects of prey migration on predators, illustrated by seasonal differences in pike foraging ecology between lake systems with prey migration and lake systems without. Specifically, differences in size structure and species composition of ingested prey were found during the prey migration period. Reduced somatic condition in lake systems with prey migration was also found, especially towards the end of the prey migration period. In line with this, the analyses also showed that potentially migratory prey species constituted a larger part of the prey community in systems that allowed migration. At the end of the study period, where prey fish have returned to the lake, this difference in somatic condition was no longer present. This is most likely a result of compensatory feeding in the predators upon return of the large number of migrating prey. Consequently, **paper I** argues that there are clear bottom-up effects of partial migration of prey fish on resident predators including changes in energy pathways through the food web and altering of community structure of prey. The impact of partial migratory prey on top predators, as illustrated in **paper I**, may be fluctuating because migrating prey are returning to the resident predators in the lake during spring. Accordingly, predators have the ability to acquire the resources and energy they lose during the period where a large percentage of their prey aggregate in connected streams outside the predators foraging habitat. The abundance of potentially migratory prey species during the lake residence period in summer is higher in lakes where prey can migrate, compared to lakes where prey are resident (**paper I**). Hence, potentially migratory species seem to have a relative competitive advantage in systems where they are able to reduce their predation pressure in winter, by migration into refuges in streams. The effect of season on the

relative contribution of potentially migratory prey species to the diet of predatory pike was more pronounced than the effects of migratory opportunity, suggesting that potentially migratory prey species are particularly vulnerable during winter, which also may explain why some prey species are more migratory than others. It is possible that the bottom-up effects caused by partial migration found in **paper I** might be a widespread phenomenon also in other ecosystems. However, the unique design of this study with eight separate predator-prey systems as replicated experimental units may be difficult to obtain in marine or terrestrial ecosystems.

2.3. Ecological effects of within and between lake movements

Focus in the previous section was on how spatial ecology of prey fish, i.e. seasonal migration of prey cause clear seasonal bottom-up effects on resident top predators, affecting the predator foraging ecology and changing the relative importance of alternative energy pathways in lake ecosystems. Contrary to migrating fish, which recurrently move between habitats often in synchrony with seasonal changes in the environment, fish dispersal and nomadism (section 2.1.2 and 2.1.4) in particular is less predictable, i.e. on an irregular or even unique basis. Thus, the possible effects and implications caused by fish dispersal and movement to their new habitat could potentially be longer lasting especially if the moving population stay in the new habitat, as is implied in the definition of dispersal (but not necessary in the definition of nomadism). In this section focus is on how spatial ecology of bream, a benthivorous species and potential bioengineer (see Box 1), can have ecological effects on lake ecosystem functioning.

In **paper II**, the aim was to investigate seasonal dynamics in adult bream activity, its potential impact on water turbidity, and thus possible resuspension effects, under natural conditions in a shallow freshwater lake (Fig. 2). Bream daily movement within the lake was studied using passive integrated transponder (PIT) technology (see section 4.1, Fig. 4) during a period of four consecutive years. Water turbidity and temperature was also measured daily during the same period of time using a turbidimeter. Results from **paper II** illustrated a clear relationship between bream movement and water turbidity, especially during the winter season where water temperatures were below 15°C. Interestingly, there was no apparent relationship between bream movement and turbidity at higher temperatures, and I argue that this is because phytoplankton productivity in the lake most likely is the main driver of turbidity during spring and summer. Hence, the relationship between bream movement and water turbidity may still exist at higher water temperatures (above

15°C) but its effect on increased sediment suspension is masked by increased phytoplankton production. This confirms that large bream, on the basis of its feeding strategy, are indeed important ecosystem engineers, especially in shallow lakes, and during winter. Proposing, that the effects could be most profound during early spring when the submerged macrophytes are small and dependent on optimal light conditions near the sediment surface and thus vulnerable to spring bream activity. Likewise, King & Hunt (1967) argued that benthivorous carp in enclosures had strong impacts on submerged vegetation in May when the vegetation was still young. It is well established that submerged macrophytes play an important role in stabilizing shallow lakes in a clear water state (Scheffer et al., 1993; Jeppesen et al., 1997), i.e. they bind nutrients and reduce sediment resuspension by wind (Donk & Bund, 2002; Nurminen & Horppila, 2009). Hence, winter season activity of bream may play a role for maintaining lakes in a turbid state, by preventing spring establishment of submerged macrophytes. Ultimately, this can lead to reduced biodiversity as submerged macrophytes promote species diversity by providing habitat and food resources for a range of organisms (Declerck et al., 2007).

As introduced in section 2.1.4, movement patterns of adult benthivorous bream between two shallow lakes was studied in **paper III** using passive integrated transponder (PIT) technology (section 4.1, Fig. 4) and a data series of nine contiguous years. The seasonal and daily movement patterns as well as the percentages of the population that annually moved from one lake to another were studied. Furthermore, the return patterns, i.e. if and when bream return to the lake in which they were tagged, was explored. The results in **paper III** demonstrates that bream indeed move between the two lakes (Fig. 2), consistent with previous, more general studies (Molls, 1999; Lucas & Baras, 2001; Lilja et al., 2003). More importantly to ecosystem dynamics, occasionally a considerable part of the bream populations are involved in these inter-lake movements. For example, in 2008 more than 37% of the population of adult bream in Lake Viborg moved upstream to the neighboring Lake Loldrup and a substantial part of these stayed there for at least a year. Clearly, such sudden increases in the amount of benthivorous bream are likely to have strong impact on lake ecosystems. In fact, although only anecdotally described, Lake Loldrup was less turbid in 2007 and had good coverage of macrophytes but this changed after the 2008 movement event. Turbidity increased and submerged macrophytes disappeared. It is likely that this change was a result of increased foraging activity from the increased bream population, causing sediment disturbance resulting in the decrease or total extinction of submerged macrophytes as well as resuspension of sediment and nutrients into the water column. Such a large change in the

community composition introduced in a short period may have increased phytoplankton density and promoted the tipping point to change the ecological state of the lake.

Before ending this chapter it is relevant to highlight the findings in **paper III** regarding the nomadic movement behavior of large adult benthivorous bream. This nomadic behavior, unpredictably in time and space between neighboring lakes, can have consequences for our understanding of alternative stable state theory in shallow lakes.

Box 1

Benthivorous feeding behavior and the impact on water clarity

Benthivorous fish, such as adult bream, can play an important role in the eutrophication process in lakes. Large bream forage by penetrating and probing the lake sediment searching for prey. During this process, bream capture sediment particles along with their prey. The prey are selectively retained, while sediment particles are passed through the gill-raker system and flushed back into the water column (Lammens & Hoogenboezem, 1991). This foraging behavior has the potential to cause profound resuspension of lake sediments (Winkel & Davids, 1985; Breukelaar et al., 1994; Zambrano et al., 2001; Parkos et al., 2003) by increasing water turbidity due to increased inorganic suspended material released from the sediment and hence, the water clarity and light penetration through the water column is reduced (Roberts et al., 1995; Parkos et al., 2003). Also, nutrients otherwise trapped in the sediment are released back into the water column due to resuspension caused by foraging activity of these benthivorous fish. Resulting in increased input of total phosphorus and nitrogen concentrations to the water column, which ultimately can lead to increased growth of algal biomass (Boström et al., 1982; Andersson et al., 1988; Parkos et al., 2003; Fisher et al., 2013; Gu et al., 2016). The reduction in water visibility due to suspended material and planktonic algal growth affects dispersal and growth of submerged macrophytes and may also influence foraging behavior of visual predators (including piscivores fish; Fisher et al., 2013; Gu et al., 2016). Furthermore, benthivorous fish can negatively affect submerged macrophytes directly by uprooting due to physical disturbance of sediment when searching for food. Such uprooting may reduce existing submerged macrophyte densities and prevent the establishment of new macrophytes (King & Hunt, 1967; Roberts et al., 1995; Parkos et al., 2003), limiting the important stabilizing role macrophytes play in shallow lakes (Donk & Bund, 2002; Nurminen & Horppila, 2009). Hence, benthivorous fish, such as adult bream can play an important role for maintaining lakes in a turbid stable state. With this motivation, **papers II and III** of this thesis characterized large benthivorous fish as bioengineers - organisms that can have significant impact on the physical conditions in lake habitats.

This theory predicts that ecosystems may occur in alternative stable states and that shifts between states are abrupt, not gradual. Based on the observations from **paper III**, it could be argued that between-lake movements of bream such as the one observed in 2008 has potential to play a role for sudden alterations in stable states in shallow lakes.



*Figure 2: Study system of **paper II** and **III**.*

Top left picture: Lake Loldrup (56°29'N, 9°26'E) is a small and shallow lake (area of 0.39 km², average depth of 1.2 m) surrounded by farm land.

Bottom left picture: Lake Viborg (56°26'N, 9°25'E) is a larger lake consisting of two basins. The northern basin is marginally smaller and deeper (1.23 km², average depth of 7.0 m) than the southern basin (1.46 km², average depth of 3.4 m). The two basins are separated by a 50 m long and 6 m wide stream without barriers.

Right picture: Section of the 2.2 km long stream (width; range 2-6 m, slope; mean 0.02%, depth; range 0.5-1.5 m) connecting Lake Loldrup and Lake Viborg (northern basin). No physical obstructions are located in the stream.

3. APPLIED ASPECTS OF SPATIAL ECOLOGY

In chapter 2, the potential direct and indirect implications of spatial ecology on lacustrine fish on lake ecosystems was discussed, primarily in relation to the findings in **papers I, II, and III**. The aim of this chapter is to place the findings about bream movement patterns (**paper II and III**) and seasonal migration of cyprinids (**paper IV**) into an applied context. Considering that **paper IV** focus on lake restoration, the first section is an introduction to lake restoration after which the findings from **paper IV** is discussed in that context. Next, applied lessons learned from **paper III** are discussed, i.e. how inter-lake movement of bream potentially can influence our perception of previous biomanipulation efforts as well as what to take into consideration in future biomanipulation projects.

3.1. Lake restoration and biomanipulation

Lake restoration is defined as any active attempt to return an ecosystem to earlier condition before degradation resulting from any kind of disturbance (Welch & Cooke, 1987). Lake restoration can refer to methods implemented within the lake as well as measures taken outside the lake, such as reduction of external nutrient loading by improving wastewater treatment (National Research Council, 1992). Throughout the past 40-50 years a significant number of lake restoration projects have been conducted to combat eutrophication (Perrow & Davy, 2002; Cook et al., 2005; Bernes et al., 2015). Numerous lake restoration techniques have been developed to overcome the chemical or biological resistance of an eutrophicated state (Cooke et al., 1993; Meijer et al., 1999; Gulati & Van Donk, 2002; Lathrop et al., 2002). Principally, the methods of lake restoration can be divided into two types; physiochemical and biological methods (Søndergaard et al., 2007). Physiochemical methods aim to reduce phosphorus availability, that is, reduce the phytoplankton biomass by nutrient limitation. These methods include sediment dredging where phosphorus rich sediment is removed to reduce the internal loading of phosphorus (Van der Does et al., 1992), sediment fixation with iron, aluminium, calcium or other phosphorus-binding agent to decrease the internal phosphorus release (Søndergaard et al., 2007), and hydrological measures, such as flushing, where nutrient poor water is flushed into the lake to decrease phosphorus concentrations (Jagtman et al., 1992), or hypolimnetic oxygenation in order to reduce the accumulation of phosphate in deep waters (Gächter & Müller, 2003). Biological methods to improve eutrophic lakes involve removal of zooplanktivorous and/or benthivorous fish to increase the number of large zooplankton and their

grazing in phytoplankton (Meijer et al., 1999; Søndergaard et al., 2007) and reduce resuspension of sediment caused by benthivorous foraging activity. In addition, stocking of predatory fish (Jacobsen et al., 2004; Skov & Nilsson, 2007), such as pike, has been used in order to reduce the number of zooplanktivorous fish and improve zooplankton biomass and thus increase the predation pressure on phytoplankton and increase macrophyte establishment (Ozimek et al., 1990). Furthermore, protection from plant-eating birds or fish to maintain high macrophyte coverage, and introduction of mussels to increase the filtration of lake water and with it create clearer water are possible methods (Reeders & Bij de Vaate, 1990). These biological lake restoration methods are also referred to as biomanipulation and mass removal of fish are the most common technique in lake restoration of eutrophic lakes, at least in Denmark (Søndergaard et al., 2007; Søndergaard et al., 2008). Lake restoration can be a significant tool to improve water quality within lakes and most reported restoration initiatives have led to improvement. However, the longevity of the improvements varies considerable and documentation on long-term effects (6 to 10 years) is relatively limited, and descriptions are usually restricted to single lake studies (Van de Bund & Van Donk, 2002; Hansel-Welch et al., 2003; Loughheed et al., 2004; Ibelinges et al., 2007; Søndergaard et al., 2008).

3.1.1. Biomanipulation by fish removal

Biomanipulation by fish removal is the most often used biomanipulation method in Denmark (Søndergaard et al., 2007). The principle behind biomanipulation by fish removal is based on utilization of biological interactions within lakes in order to improve grazing on algae by zooplankton and eliminate fish species that recycle nutrients. The concept of biomanipulation by fish removal was formally defined by Shapiro et al. in 1975, who wanted an alternative approach to the at the time conventional nutrient management relying on chemicals and engineering. One such method to reestablish eutrophicated lakes into a clear water state by means of biomanipulation is by removing planktivorous and benthivorous fish from the lake. Zooplanktivorous fish such as roach and young bream feed on zooplankton and by removing a large proportion of the zooplanktivorous fish biomass in the lake, the predation pressure on zooplankton is reduced substantial and hence, the possibility for zooplankton to control/reduce phytoplankton biomass is enhanced. Thus, by altering the fish community composition in the lake by removing zooplanktivorous fish, one also alters the entire ecosystem structure through cascading trophic interactions. Ultimately, this should lead to an increase in water transparency and invasion of submerged macrophytes which helps to stabilize the

lake in the clear water state in line with the alternative stable state theory (Williams, 2005). In addition to removing zooplanktivores, biomanipulation also often intend to remove large benthivorous fish, e.g. bream, which cause resuspension of sediment when foraging (Breukelaar et al., 1994; Zambrano et al., 2001; Parkos et al., 2003) leading to an increase in water turbidity (Roberts et al., 1995; Parkos et al., 2003) (see also Box 1). Hence, benthivorous bream can play an important role for maintaining lakes in a turbid stable state and consequently removal of benthivorous fish can lead to increases in rooted submerged vegetation, increased water transparency as the submerged macrophytes stabilize the sediments (Donk & Bund, 2002; Nurminen & Horppila, 2009).

In order to obtain notable effects to establish cascading influences, more than 200 kg ha⁻¹ fish have to be removed within a few years (Olin et al., 2006; Søndergaard et al., 2008). However, biomanipulation is most effectively applied in small and shallow lakes and in most cases it is not a one-time intervention. Short-term effects of biomanipulation are easier obtainable than long-term effects (Van de Bund & Van Donk, 2002; Søndergaard et al., 2007), and frequently the significant effects of fish removal were maintained for 6 to 10 years, after which many lakes tended to return to pre-restoration condition (Søndergaard et al., 2008). Sufficiently extensive removal of zooplanktivorous and benthivorous fish will elongate the clear water state, and with it, the period before further action is needed. However, biomanipulation often has to be performed multiple times in order to maintain the lake in the clear water state, at least in the most nutrient rich lakes (Van de Bund & Van Donk, 2002). Such large-scale fishing is labor intensive and costly, partly due to the unpredictable spatial distribution of targeted zooplanktivorous and benthivorous fish, and even though the maintaining procedure is generally not as comprehensive as the first intervention, it is still extensive. Accordingly, it is preferable to implement removal of zooplanktivorous and benthivorous fish multiple times to sustain the lake in a clear water state. Hence, it seems relevant to explore for alternative fish removal methods and preferably cost-effective methods.

3.2. Cost effective biomanipulation

Biomanipulation, i.e. fish removal has traditionally been performed by various methods such as seining, trawling, netting, fyke netting, or combinations of these (Lammens, 2001).



*Figure 3: Study system of **paper IV**.*

Left picture: Lake Søgård (55°25'N, 9°19'E) a small, eutrophic, and shallow lake (area 0.26 km², average depth 1.6 m, mean summer Secchi depth 0.4-1.1 m).

Right picture: Inlet stream of Lake Søgård where cyprinid fish removal occurred.

In **paper IV** the objective was to investigate if removal of cyprinid fish aggregated in streams (see section 1.3) connected to the lake during seasonal winter migration could be an efficient complementary method to the traditional in-lake fishing in biomanipulation efforts. In shallow lakes zooplanktivorous cyprinid fish species perform partial migration and migrate out of their natal lake and into connected streams during the winter period to return to the lake the following spring (Skov et al., 2008). Up to 80% of individual fish within cyprinid populations migrate out of shallow lakes during the winter season (Skov et al., 2010) and can remain in the stream for more than half of the year (Skov et al., 2008; Skov et al., 2010; see also section 1.3.2). In the light of this behavior, cyprinid fish seasonal migration could be important to consider when performing biomanipulation since these migrations results in aggregation of large amount of cyprinid fish in streams which compared to lake area is relative restricted. Furthermore, in-lake fish removal is often performed and even recommended to be undertaken in winter and early spring where a part of the cyprinid fish population migrate to the streams (Perrow et al., 1997). All in all, the findings from **paper IV** could pave the way for a potential cost effective fish removal. This was explored in a shallow eutrophic

lake, Lake Søgård (Fig. 3), where occurrence of seasonal migration of cyprinids are well established (e.g. Skov et al., 2010). In Lake Søgård roach, bream, and white bream (> 20 g) were captured using electrofishing, beach seining, and gill netting and tagged with passive integrated transponder (PIT) tags (see section 4.1; Fig. 4) in late September 2013 and 2014. Seasonal migration of cyprinid fishes along with water temperature was monitored and during the winters 2013/2014 and 2014/2015 cyprinid fish were removed from the inlet stream by electrofishing.

The results from **paper IV** showed as expected that the dominant cyprinids in the lake, i.e. roach, bream, and white bream performed partial migration. In specific, they migrated out of the lake and into the inlet stream (Fig. 3) during October and November when water temperatures fall below 6°C and returned to the lake from March to April. On average of the two years of research (seasons of 2013/2014 and 2014/2015) as much as 48%, 21%, and 36%, of the populations of roach, bream, and white bream, respectively was present in the stream from November to April. The maximum proportion of cyprinid fish present at any point during the two winters varied between species and year, but ranged between 29 and 73%. This illustrate that a high share of the cyprinid populations can potentially be target by winter fish removal in streams.

Based on mark-recapture density estimates it was obtainable to remove 27%, 5%, and 35% of the roach, bream, and with bream population, respectively, with the use of maximum 90 man hours the first year (2013/2014) of executing fish removal in the stream. In the second year (2014/2015) of the research it was obtainable to remove approximately 10%, 3%, and 20% of the roach, bream, and white bream population, respectively, with the use of only 18 man hours. Even though the percentage of fish removed varied, it was possible to remove up to 35% of the zooplanktivorous cyprinids annually from Lake Søgård, with relatively small endeavors. However, depending on species and study year more than 70-80% of the cyprinids were monitored aggregating outside the lake for shorter or longer periods during winter. Hansson et al. (1998) suggest that cyprinid populations should be reduced by at least 50% in order for biomanipulation efforts to result in detectable changes in the trophic structure of lakes. Hence, given maximum fishing success in the inlet stream of Lake Søgård this number could potential have been reached, at least for some of the cyprinid species. Most cyprinid fish were situated in the inlet stream at water temperatures below 6°C however, during the mid-winter when temperatures dropped below 2°C a percentage of cyprinids returned to the lake. The return of cyprinids to the lake when temperatures dropped below 2°C may be caused by ice over on the lake which can influence migratory behavior of cyprinid fishes (Heermann & Borcharding, 2006). In summary, it is tentatively suggested that fish removals

are most efficiently done at water temperatures below 6°C but before ice cover establish on the lakes. Furthermore, local knowledge is also needed to establish if winter migration mainly take place in the lake inlets, outlets, or in both, as previous studies have shown that this can vary between lakes and within season (Skov et al., 2008; Skov et al., 2010).

Another central finding in **paper IV** is that the propensity to migrate varied with body size for all three species. The inclination to migrate out of the lake increased with body size for roach, whereas it declined with body size for both bream and with bream. These results support other studies that large benthivorous bream do not migrate out of the lake, probably because they have outgrown the gab size for their predators and then no longer are in high risk of predation in the lake during the cold season (Skov et al., 2011). Since bream, and especially large bream often is an important target species in biomanipulation measures (e.g. Søndergaard et al., 2008), the fact that large individuals rarely perform seasonal migration confirms that stream fish removal cannot stand alone, but should be considered a complementary method to in-lake fish removal.

In **paper IV** some evolutionary considerations related to selectively fishing for the migratory parts of the populations of cyprinids is also presented. Since this method only capture the cyprinid fish performing winter migration it may lead to a decrease in the proportion of migratory fish in the population and microevolutionary changes leading to a higher frequency of resident fish could be expected. Since the proportion of winter migratory planktivorous affect zooplankton average size over winter and subsequently timing of phyto- and zooplankton peaks in spring (Brodersen et al., 2011), which models suggest should affect the occurrence, timing, and duration of clear-water phases in spring and thereby the (re)establishment of macrophytes (Brodersen et al., 2008b), increasing the proportion of resident fish may counteract the objective of the biomanipulation.

In summary, **paper IV** therefore concludes that it is possible to utilize the fact that the majority of cyprinid fish migrate out of the lake and aggregate in restricted areas within the stream as a supplementary tool for biomanipulation.

3.3. Implications of inter-lake movements of large bream on biomanipulation measures

Activity of large bream in lakes can influence water turbidity why bream can be considered a bioengineer in shallow lakes (see Box 1). In **paper II**, this is supplemented by showing that even during periods with water temperatures below 15°C, bream activity influences water turbidity with

potential negative consequences for the shallow lake ecosystems. Hence, the results from **paper III** show that large benthivorous bream may move in large numbers between lakes, can have strong implications for designing best practice biomanipulation measures in the future as well as our understanding of the success of previous biomanipulation attempts. With regards to the latter, the demonstration of between lake movements might extend our understanding of the longevity of previous performed biomanipulation efforts, i.e. why some lakes within relatively few years return to a turbid state after fish removal (Søndergaard et al., 2008). If one lake is connected to one or more lakes, the longevity of biomanipulation could be influenced of bream moving in from the nearby lake(s). Both study lakes in **paper III**, Lake Loldrup and Lake Viborg, have been attempted to restore by fish removal at various times since the mid-1990s (Johansson et al., 2006; Viborg Municipality, 2016). Interestingly, the longevity of these restoration projects have, in general, been short lasting, and seen in the light of the results from **paper III**, this could be influenced by inter-lake movements of large benthivorous bream. If the phenomenon of nomadism movement patterns of bream, and thereby frequent but unpredictable bream movements between lakes described in **paper III**, apply to other lake systems, it would be advisable to take this into account in future biomanipulation projects. One obvious first step would be to include monitoring of between lake movements during and following the biomanipulation efforts, in order to determine to what extent between-lake movements occur. Second, if emigration of bream is established this knowledge could be combined with removal initiatives, e.g. placing large fyke nets in the tributaries with their opening facing away from the lake of interest. In theory, these nets could catch bream moving towards the lake and ultimately result in cost effective removals compared to removal of large benthivorous bream within the lake.

4. METHODS

4.1. PIT telemetry

Active and passive telemetry methods are often used when exploring spatial ecology of fish (Lucas & Baras, 2001). Using actively telemetry methods requires that the fishes are tracked actively, whereas in passive telemetry data are collected from stationary (passive) listening stations (e.g. Chapman et al., 2012). In this thesis passive telemetry is a key method, why I introduce and discuss the method below.

Passive integrated transponder (PIT) devices were first used in the mid-1980s (Gibbons & Andrews, 2004). Using PIT tags in wild animals actually began with fisheries studies to determine the efficacy of the method for measuring fish movement (Prentice & Park, 1983). Since, it has been used successfully to study a diversity of animal groups, such as small mammals (Harper & Batzli, 1996), birds (Jackson & Bünger, 1993), amphibians, and reptiles (Camper & Dixon, 1988). PIT tags consist of a small electromagnetic coil and encoded microchip encased in biocompatible glass. The tags remain passive until activated by an electromagnetic field sent from a detector, and when activated, it transmits a unique serial number to the reader. The operational time of PIT tags is accordingly expected to last for the lifetime of the tagged animal, making this technique ideal for long-term studies (Gibbons & Andrews, 2004). The advantages of PIT tags are numerous; the tags are small, internal, permanent, and have virtually no negative impact on animals. They are inexpensive compared to other electronic tags, enabling large sample sizes (Gibbons & Andrews, 2004; Skov et al., 2011). Research using PIT tags can provide valuable information at individual, population, and community level. The method can be used to identify growth rate, survival, and migration behavior. In order to gain this information tagged animals have to be recaptured, which is not always possible. However, often PIT tags are used in combination with automated stationary monitoring systems, which can be set up to simultaneously record temporal and spatial information, making recapture unnecessary in migration and survival studies. This method requires placing a PIT tag reader along the animals presumed path, such that the tagged animal will pass within the electromagnetic field and hence within reach of the reader. Accordingly, this setup is primarily suitable when studying animals living in defined areas, which is the case in this thesis where tagged fish in in- and outlet streams or in a lake are studied. Such a stationary monitoring system permits assessment of daily activity patterns of tagged fish by storing the individual ID number of the tag with the time and date of detection on a memory card when a tagged individual is passing the

reader. In the streams, two consecutive antennas are placed a few meters apart covering the entire cross-section enabling to determine the direction of fish movement (Fig. 4). The two stationary PIT stations each consists of a loop shaped antenna and constructed by oxygen free cobber loudspeaker cable ($2 \cdot 4 \text{ mm}^2$) mounted inside a frame of 30 mm PVC pipe, which are placed perpendicular to the lake bed by wooden posts. When used in the studies presented in this thesis, PIT tagging always took place in autumn, when water temperatures were relative low ($8.7 - 15.5^\circ\text{C}$), but still before the seasonal migration were initiated. Fish $\geq 20 \text{ g}$ in wet weight (Skov et al., 2005) were target organisms, and tagged with PIT tags (Texas Instruments, RI-TRP-RRHP, Plano, Texas, USA, half duplex, 134 kHz, 23.1 mm long, 3.85 mm in diameter, 0.6 g in air) implanted manually in the body cavity using a scalpel to make a small incision posterior to the pectoral fin. Even though, small individual size of fish may preclude the use of PIT tags, effects on growth and survival in these studies are assumed to be negligible due to the minimum size (20 g in weight) of tagged fish (Skov et al., 2005).

As mentioned, PIT antennae systems are often used to monitor fish movements in streams (e.g. Aarestrup et al., 2003; Hodder et al., 2007). However, the study in **paper II** illustrates that PIT systems also have the potential to further our knowledge about fish behaviour within a lake. Although used within lakes before in relation to explore fish use of artificial structures (Russel et al., 2008; Goldsmith et al. (poster)) **paper II** may represents the first study that use PIT antennae systems to explore open water movements. In this study, the lake antennas were positioned in a setup similar to the one used in streams (**papers I, III, and IV**), i.e. they are also set in pairs. However, they are not placed parallel to each other, but instead each pair of antennas was composed of one antenna in the interface between vegetation and open water and one antenna on average 30 meter further ashore in the limnetic zone. PIT antennae systems in lakes can undoubtedly be a future valuable alternative to active telemetry methodology that so far has been the dominant telemetry method used in lakes (e.g. Jacobsen et al., 2002; Andersen et al., 2008; Bajer & Sorensen, 2010).

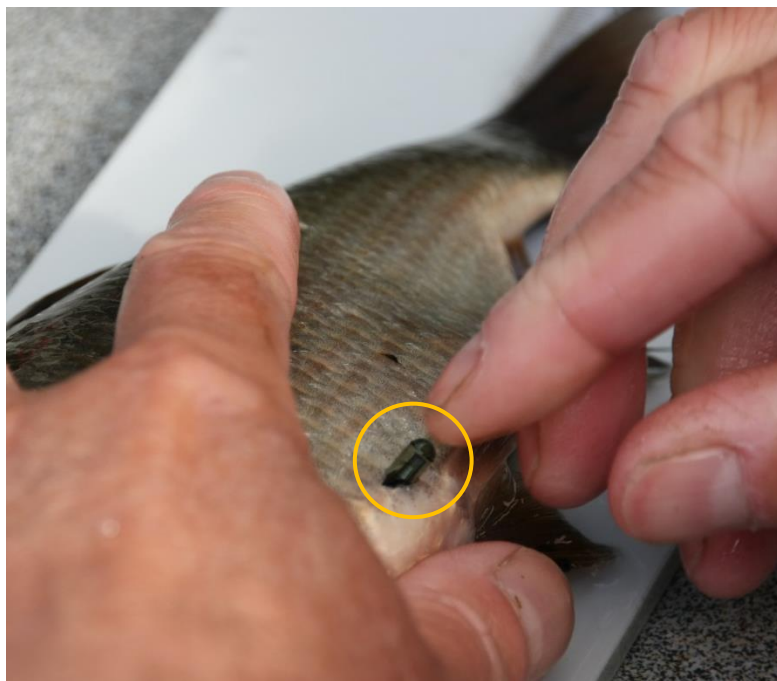


Figure 4: PIT telemetry.

Top picture: Loop shaped stationary PIT stations (yellow squares) placed few meters apart covering the entire cross-section of the stream.

Bottom left picture: 23.1 mm long PIT tag (Texas Instruments, RI-TRP-RRHP, Plano, Texas, USA, half duplex, 134 kHz, 3.85 mm in diameter, 0.6 g in air).

Bottom right picture: PIT tag implanted into the body cavity of the fish.

4.2. Stomach content analysis

In **paper I** stomach content of 627 pike (total length (mm), range: 335-1017) were analyzed in order to categorize and compare ingested prey biomass of pike between season in lakes with or without migrating prey fish. Traditionally, such studies have sacrificed the fish to examine their stomach contents. However, sacrificing fish for food habit studies may cause poor public relations and may not be a preferable option if study fish are economically valuable, or come from a low density population (Baker & Fraser, 1976; Crossman & Hamilton, 1978; Light et al., 1983; Haley, 1998). Additionally, lethal methods may significantly alter the population structure of fish in some areas (Light et al., 1983; Hartleb & Moring, 1995). Therefore, various non-lethal methods have been developed to assess food habits of fish (Kamler & Pope, 2001). All stomach contents of pike in **paper I** were collected by a stomach-flushing method, called gastric lavage, since this method show the most effective method of recovering (Kamler & Pope, 2001). Furthermore, the gastric lavage method has been a widely used technique for obtaining the stomach content of live fish (Hyslop, 1980) and is known to provide close to 100% retention of stomach content (Light et al., 1983). Immediately after capture, when still paralyzed from electrofishing, pike stomach content was flushed using a hand pump. A rigid plastic tube was connected to the pump and inserted into the stomach of the pike through the mouth and esophagus. Pike were held dorsal-side-up and with the head angled downward to facilitate food removal. Water was pumped continuously into the stomach causing food items to be regurgitated.

Each stomach content sample collected in the field was stored frozen until analyzed in the laboratory where they were thawed before prey fish were identified to the lowest recognizable taxonomic level. Individual prey length (nearest mm, standard length) was measured. If the prey fish were partly digested the length was estimated using species-specific length-weight relationship obtained from prey fish sampled during the same experiment which were used to estimated prey availability of pike in the lakes (Table 1). Wet weight of prey fish were likewise estimated on the basis of the prey availability study from species-specific length-weight relationships. Based on these, total prey biomass as well as potentially migratory prey biomass per individual pike stomach was estimated.

Table 1: Species-specific length-weight relationships obtained from prey availability study. Number in () next to species name is number of fish used to estimate the relationships. Parameters used is standard length (SL), total length (TL), caudal fin length (CF), body depth (BD) all measured in mm and weight (W) measured in g.

	Roach (4966)	Bream (158)	White bream (16)	Perch (1402)	Pike (23)	Three-spined stickleback (21)
Standard length	$3.57 \cdot CF + 4.87$ $R^2=0.96$	$3.04 \cdot CF + 3.73$ $R^2=0.92$	$2.87 \cdot CF + 11.84$ $R^2=0.96$	$4.36 \cdot CF + 11.26$ $R^2=0.79$	$4.52 \cdot CF + 46.80$ $R^2=0.75$	
Standard length	$0.79 \cdot TL + 0.66$ $R^2=1.00$	$0.76 \cdot TL - 0.17$ $R^2=1.00$	$0.75 \cdot TL + 2.38$ $R^2=1.00$	$0.83 \cdot TL + 0.71$ $R^2=0.98$	$0.85 \cdot TL + 0.60$ $R^2=0.99$	$0.76 \cdot TL + 4.69$ $R^2=0.99$
Standard length	$40.80 \cdot W^{0.30}$ $R^2=0.99$					
Weight	$4 \cdot 10^6 \cdot SL^{3.35}$ $R^2=0.99$	$5 \cdot 10^6 \cdot SL^{3.32}$ $R^2=0.99$	$2 \cdot 10^5 \cdot SL^{3.07}$ $R^2=0.97$	$8 \cdot 10^6 \cdot SL^{3.21}$ $R^2=0.98$	$1 \cdot 10^5 \cdot SL^{2.95}$ $R^2=0.89$	
Weight	$4 \cdot 10^6 \cdot TL^{3.16}$ $R^2=0.98$	$2 \cdot 10^6 \cdot TL^{3.31}$ $R^2=0.99$	$1 \cdot 10^5 \cdot TL^{3.02}$ $R^2=0.98$	$8 \cdot 10^6 \cdot TL^{3.07}$ $R^2=0.94$	$9 \cdot 10^6 \cdot TL^{2.95}$ $R^2=0.89$	
Body depth	$0.34 \cdot SL - 4.04$ $R^2=0.98$	$0.46 \cdot SL - 9.95$ $R^2=0.97$	$0.43 \cdot SL - 6.18$ $R^2=0.99$	$0.33 \cdot SL - 3.05$ $R^2=0.96$	$0.17 \cdot SL + 2.70$ $R^2=0.85$	
Body depth	$0.27 \cdot TL - 3.78$ $R^2=0.98$	$0.35 \cdot TL - 10.54$ $R^2=0.97$	$0.32 \cdot TL - 5.20$ $R^2=0.99$	$0.28 \cdot TL - 3.41$ $R^2=0.97$	$0.14 \cdot TL + 3.09$ $R^2=0.86$	

4.3. Stable isotope analyses

Combining stomach content and stable isotope analyses will provide a robust short- and long-term estimate of diet. The stable isotope ratio of carbon ($\delta^{13}C$) provides a time-integrated measure (over weeks to months) of an organism's feeding ecology, in contrast to the traditional 'snap-shot' picture provided by stomach content analyses and furthermore, have the potential to track energy flow through food webs (Hobson et al., 1995; Post, 2002). Hence, it is important to state, that stable isotope analysis of tissue samples do not provide a dietary detailed analyses, but gives a broad overview of diet over longer timescale and includes all assimilated food.

Samples of white muscle tissue (216 ± 94 mg wet weight, mean \pm SD) free of skin and bones taken anterior to the dorsal fin were prepared for stable isotope analysis. White muscle tissue was used for stable isotope analysis because of its low tissue turnover rate (Rounick & Hicks, 1985, Hesslein et al. 1993). All muscle samples were dried to constant mass at 55°C for 48 hours. The dried samples were kept in a desiccating cabinet containing silica gel until further analysis. Dried muscle samples were homogenized using a TissueLyser II (QIAGEN®) grinder. Approximately 0.5 mg (dry mass)

of sample (0.47 ± 0.03 mg, mean \pm SD) was weighed into pre-weighed tin capsules ($5 \cdot 9$ mm). Stable carbon isotope analyses were performed at the Swiss Federal Institute of Aquatic Science and Technology (Eawag), Center for Ecology, Evolution and Biogeochemistry (CEEB), Switzerland. Samples were combusted in a Flash 2000 element analyzer coupled to a Delta V Advantage isotope ratio mass spectrometer via a ConFlo IV interface. Standards for $\delta^{13}\text{C}$ were calibrated against Vienna Pee Dee Belemnite (VPDB). The crimped tin capsules were introduced via a solid autosampler and combusted at 1000°C in a reactor packed with chromium oxide and silvered cobaltous/cobaltic oxide. Following combustion, oxides were removed in a reduction reactor (reduced copper at 650°C). A post-reactor gas chromatography column was kept at 65°C for separation of evolved N_2 and CO_2 before entering the isotope ratio mass spectrometer. Stable carbon isotope ratio was expressed in conventional δ notation in parts per thousand (‰) as a measure of heavy to light isotope using:

$$\delta^{13}\text{C} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000,$$

where R is the ratio of $^{13}\text{C}:^{12}\text{C}$.

4.4. Measurement of water turbidity

Turbidity is caused by particles in water and is a measure of a specific portion of a light beam passing through water is deflected from undissolved particles. Accordingly, the more total suspended solids there is in the water, the less transparent the water will be and consequently the higher the turbidity. The diffusion of light caused by undissolved particles in the water to a lesser or greater degree of the deflection depends on; the type of particles and hence absorbance, the size and shape of particles, and the concentration of particles.

Water turbidity was measured using AQUAlogger® 210TYT, Aquatec, Basinstroke, UK (300 mm long x 60 mm, diameter). The turbidimeter was attached to a fixed structure (wooden pole) in the lake approximately 0.5 meters below the water surface and measured water turbidity in Formazin Turbidity Units (FTU). Turbidity was measured using optical backscatter, which detect optical scattering of infrared light from suspended matter. The AQUAlogger® 210TYT uses an 850 nm light source and, within the range of 0-750 FTU it measures turbidity linearly with a deviation of $< 2\%$. To avoid biological growth on the optical window of the logger, it was equipped with an antifouling wiper. The turbidimeter was set to measure turbidity five times minimum every second hour during the study period. In this way, the advantage of using a turbidimeter is namely the

possibility to program it beforehand to measure turbidity when wanted. An alternative approach would be to manually measure Secchi depth in the lake, which is very time consuming. One of the disadvantages of using a stationary turbidimeter in this setup is that water turbidity is only measured in one location of the lake. Besides, the turbidimeter unfortunately malfunctioned occasionally which lead to periods with no measurements of water turbidity.

CONCLUSION

This thesis has focused on spatial ecology of freshwater fishes and how movements of lacustrine cyprinid fish affects higher and lower trophic levels and lake ecosystem functioning in freshwater systems. Moreover, there was focus on applied aspects including how to implicate cyprinid movements as a supplementary tool in lake restoration. Conclusions of the findings presented in this thesis are listed below:

In **paper I**, the foraging ecology of an important top predator (pike) in lakes and how it was affected by seasonally fluctuating densities of prey caused by prey migration from the lake was explored. This was examined in a replicated design using full-scale freshwater lakes, four lakes with- and four lakes without opportunity for prey migration. Results showed clear seasonal bottom-up effects of prey migration on the foraging ecology of pike predators. The prey ingested by pike predators in lakes exposed to migrating prey, change in size structure and species composition during the winter season compared to ingested prey in pike predators not experiencing fluctuating prey biomass. Furthermore, pike experience a size-specific change in littoral versus pelagic origin of diet, and reduced somatic condition during the prey migration period. It is concluded that seasonal prey migrations have important implications for predator foraging ecology and may cause seasonal shifts in the importance of their supporting energy pathways.

In **paper II**, movements of adult bream within a shallow lake and specifically the impact of their activity on water turbidity was studied. The results showed a clear day-to-day relationship between activity of adult benthivorous bream and water turbidity, especially during the winter season with water temperatures below 15°C. This finding adds an important seasonal dimension to previous knowledge about the structuring role of benthivorous bream in lake systems and implies that winter season activity of benthivorous bream may play a role for maintaining lake ecosystems in a turbid state, e.g. by bringing nutrients from the benthic into the pelagic and potentially also by preventing important spring establishment of submerged macrophytes through shading or mechanical stress.

In **paper III** passive telemetry technology was used to describe long-term movement patterns of 1280 individually tagged adult benthivorous bream in a multi-lake drainage system during nine years. The movement pattern was best described as partial nomadism, where a part of the population were neither resident nor migratory, but instead moved between lakes in an unpredictable arrhythmic fashion, often with long residency in one lake before moving to the other lake. On average 15% of the tagged bream changed lake within the first year after tagging, but there

was extensive variation in the amount of moving bream between years, from 0% to 37%. In total, 30% of the bream that changed lake returned to the lake of tagging after 1 to 3 years, but the majority never returned during the study period. Since bream are important bioengineers, fluctuating densities of adult bream could cause instability in the ecological state of lakes. Further, the study proposes that lakes connected with other lakes in freshwater systems should not be treated as isolated management units.

In **paper IV**, cyprinid fish removal from streams was examined as a potential tool in biomanipulation of lakes. Cyprinids, such as roach, bream, and white bream migrate out of the lake and aggregate in relative small areas of connecting streams during the winter season. By fishing in the streams, results showed that it was possible to remove up to 35% of the estimated cyprinid biomass (excluding large bream) through the winter, and possibly even more biomass could have been removed with a more targeted fishing effort. Hence, it was demonstrated that fish removal from streams can be a cost effective tool in future lake restoration endeavors. However, not all size classes of cyprinids could be targeted in the stream, e.g. large benthivorous bream had low propensity to participate in the seasonal migration. Therefore, if large bream are the target species for lake restoration, stream fish removal should be considered as a supplement to traditional in-lake fish removal methods. Finally, it is also recommend that evolutionary effects of selectively fishing on the migrating part of the cyprinid populations are considered.

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PAPER I

Ecological consequences of animal migration: prey partial migration affects predator ecology and prey communities



Ecological consequences of animal migration: prey partial migration affects predator ecology and prey communities

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Abstract

1. Patterns of animal migration and the ecological forces that shape them have been studied for centuries. Yet ecological impacts caused by the migration, such as altered predator-prey interactions and effects on community structure, remain poorly understood, which to a large part is due to the scarcity of naturally replicated migration systems with negative controls, i.e. ecosystems without migration.
2. In this study, we test whether partial migration of certain species of prey within the overall prey community affects foraging ecology of top-predators and thereby alters energy pathways upwards in the ecosystem. We subsequently test for potential effects of the prey species-specific partial migration on prey community composition.

3. We examine predator-prey interactions in independent replicated freshwater lake systems, four with- and four without opportunity for prey migration. Specifically, we compare predator foraging mode and prey community structure in lakes where cyprinid prey fish perform seasonal partial migrations into connected streams with lakes lacking migratory opportunities for prey fish.
4. We find clear seasonal bottom-up effects of prey migration on predators, including changes in size structure and species composition of ingested prey, size-specific changes in littoral versus pelagic origin of diet, and reduced predator somatic condition (our fitness proxy) during the prey migration period. Our analyses further show that partially migratory prey species constitute a larger part of the prey community in systems that allow migration.
5. Hence, prey migrations have important implications for predator foraging ecology and may cause seasonal shifts in the importance of their supporting energy pathways. We suggest that such bottom-up effects of partial migration may be a widespread phenomenon both in aquatic and in terrestrial ecosystems.

Keywords: bottom-up effects, freshwater fish, migration, partial migration, predation.

Introduction

Migration is a widespread and important ecological phenomenon occurring across the entire animal kingdom and over a variety of geographic distances (e.g. Alerstam et al. 2003; Hays 2003; Dingle & Drake 2007; Hansson & Åkesson 2014; Brönmark et al. 2014). Animals migrate between habitats for a variety of reasons, for example to enhance foraging opportunities, improve reproductive success, or to avoid predators or parasites (Fryxell & Sinclair 1988; Bowler & Benton 2005; Altizer et al. 2011). The term migration often evokes images of spectacular seasonal movements of animal populations, and research on migration has historically mainly focused on the causes and patterns of these large-scale animal movements. Migratory animals have the potential to affect the stability and dynamics of entire ecosystems, by altering energy and nutrient pathways within and between their alternative habitats (Bauer & Hoye 2014; Hansson & Åkesson 2014). When considering ecological effects associated with animal migrations, the arriving species has primarily been in focus. Yet, individuals arriving to one habitat are, however, undeniably linked to departure from another. Hence, when migratory animals are dominant or keystone species in their

respective ecosystems, both their arrival and departure may have potential impacts on food-web structure and trophic dynamics.

A couple of recent studies have demonstrated trophic top-down effects of predator migration on lower trophic levels (Brodersen et al. 2008a; Post et al. 2008), but studies of ecological bottom-up effects caused by seasonal departure of migratory prey are scarce (see, however, Brodersen et al. 2015 for trophic diversification effects). Such effects should nevertheless be expected, especially since many predators do not follow migrating prey (Fryxell & Sinclair 1988; Sinclair 2003). This has previously been hypothesized to affect predator feeding rates (Fryxell et al. 2007), and here we further hypothesize that it may also affect energy pathways in ecosystems and prey community structure. However, a key challenge when studying the effects of migration in the wild is to achieve replication at the level of populations and ecosystems and to have negative controls, i.e. similar systems without migration. Due to their distinct geographic borders and spatial replication, freshwater lakes and the predator-prey interactions occurring within their fish communities are ideal natural systems for replicated study designs. Especially seasonal fish migrations from lake ecosystems to connected streams provide a powerful opportunity for cross-population studies on the consequences of animal migration (Brönmark et al. 2008).

Migrations of cyprinid fish have received considerable attention during the last decade (e.g. Jepsen & Berg 2002; Brönmark et al. 2008; Brodersen et al. 2008b; Skov et al. 2011). These fish migrate from their natal lakes into connected streams to overwinter and then return to the lake habitat in spring (Jepsen & Berg, 2002; Skov et al., 2008). The migrations are driven by seasonal shifts in the trade-off between predator avoidance and growth opportunities in lakes and streams (Brönmark et al. 2008). Cyprinids generally leave the lake when the ratio between predation risk and growth opportunity becomes lower in the streams than in lakes during autumn (Brönmark et al. 2008; Brodersen et al. 2008b; Skov et al. 2014; Hulthén et al. 2015). This is caused by substantial reductions in potential growth rate at low temperatures in combination with sustained predation from pike (*Esox lucius*), which does not follow the migratory prey into the streams over winter (Skov et al. 2008; Skov et al. 2011). Migration in cyprinid fishes is commonly partial (Chapman et al. 2012), i.e. not all individuals migrate due to intra-population differences in predation vulnerability (Skov et al. 2011), personality (Chapman et al. 2011) and size and energetic status (Brodersen et al. 2008b). Despite this variation, a significant proportion of prey fish migrate from

shallow lakes during winter, which would be predicted to have powerful implications for predators that remain resident in the lake habitat. This has yet to be empirically demonstrated and is a major focus of the present study.

The two other main objectives of this study are to examine how partial migration of prey affects 1) prey fish community structure as a consequence of species specific ability to escape predation risk during winter, and 2) possible alterations of the relative reliance on the littoral and pelagic food chains in the energy flow from primary producers to top-predators. We explore these objectives using a replicated design, where we compare the foraging ecology of piscivorous pike between four lakes with opportunity for seasonal partial migration for prey fish and four lakes without migration opportunity, i.e. where all prey fish remain resident in the lake throughout the year. Overall, we predict that predators in systems where prey can migrate will have different feeding patterns over seasons compared to predators in systems where prey migration is not possible, resulting in different relative reliance on alternative trophic energy pathways as well as affecting predator fitness components differently. Specifically, we predict that (1) prey availability will be reduced during the migration period in lakes where prey are able to migrate, (2) predators in lakes with prey migration will have lower fish prey biomass in their stomachs during the migration period, (3) the diet of predators in systems with prey migration will be dominated by smaller prey during the migration period since migratory propensity in the main prey fish, roach, increases with size (Brodersen et al. 2008b), (4) predators from systems with migrating prey will have a higher dependence on littoral food resources during the migration period, as migratory prey species generally inhabit open water while non-migratory prey species are more littoral (Skov et al. 2008), (5) the predicted decrease in prey availability during the migration period in lake systems where prey have migration opportunity will lead to reduced predator somatic condition and, finally, (6) migratory prey species will be relatively more abundant in lakes where they have the ability to migrate during winter.

Materials and methods

Study system

We evaluated seasonal changes in the feeding patterns of predatory pike in a total of eight shallow, eutrophic lakes in Denmark and Sweden (Table 1). All focal lakes contain populations of cyprinid prey fish along with other prey fish species, predominantly perch (*Perca fluviatilis*). Pike is the dominant top predator in all lakes. Four of the lakes have connected in- and outlet streams to which cyprinid fish populations partially migrate during winter. These lakes are hereafter referred to as *open lakes*. The remaining four lakes have no connected inlet or outlet streams, ruling out migration from these systems, and these lakes are hereafter referred to as *closed lakes*. Partial migration has been reported in all of the open lakes (Jepsen & Berg 2002; Skov et al. 2008; Skov et al. 2010; Skov et al. 2014; Brodersen et al. 2014). In Lake Loldrup, Lake Søgård, and Lake Krankesjön seasonal patterns of prey migration have been closely monitored for the last 11-14 years, including the year of the current study.

We sampled each lake on five occasions from August 2011 to May 2012. Based on previous data on the migratory patterns of the cyprinid prey fish species (i.e. Skov et al. 2008; Skov et al. 2010; Skov et al. 2014; Brodersen et al. 2014) we characterized the time periods as *pre-migration*, *early migration*, *mid-migration*, *late migration*, and *post-migration* (Table S1, supplementary material).

Table 1: Area (km²), depth (m), mean summer secchi depth (m), and type of lake (migration opportunities (open) and non-migration opportunities (closed)) of the eight study lakes.

Lake	Lake type	Position	Area (km ²)	Depth (m)		Mean secchi depth (m)
				Max	Mean	
Fjällfotasjön	Closed	55°31'N, 13°18'E	1.55	2.5	1.4	0.4
Hale	Closed	56°36'N, 9°35'E	0.10	1.1	0.8	Bottom
Havgårdssjön	Closed	55°29'N, 13°21'E	0.54	5.8	3.1	1.1
Udbyover	Closed	56°39'N, 10°12'E	0.21	2.6	1.1	0.8
Krankesjön	Open	55°42'N, 13°28'E	3.38	3.0	1.0	1.6
Loldrup	Open	56°29'N, 9°26'E	0.39	3.3	1.2	1.1
Stigsholm	Open	55°58'N, 9°29'E	0.21	1.2	0.8	0.9
Søgård	Open	55°25'N, 9°19'E	0.27	2.7	1.6	0.6

Sampling of predators

A total of 627 pike (total length (mm) range = 335-1017) were caught by electrofishing in the littoral zone of the lakes during the study (Table S1). We excluded smaller pike, since they may not be fully piscivorous (Skov et al. 2003). Upon capture, while still unconscious, pike were individually weighed (± 1 g), measured (nearest mm, total length), the stomach contents were collected by gastric lavage (Light et al. 1983), and a muscle biopsy of white muscle tissue for isotope analyses was removed anterior to the dorsal fin (Schielke & Post 2010), after which pike were released on the capture location. Stomach content and muscle samples were frozen for later analyses upon return to the laboratory.

Prey availability

On each sampling occasion, five randomly chosen transects in the littoral zone of each study lake were electrofished for five minutes each. All potential prey fish (see below) caught in each transect were frozen and stored for later analysis in the laboratory, where individual prey fish were identified to species, and individually weighed and measured (to nearest mm). Prey availability was then estimated for each lake and each of the five time periods by calculating the mean catch for the five electrofished transects per minute. Only fish with body depths below the gape-size limit (Nilsson & Brönmark 2000) of the average size of pike (574 mm) were included in the calculation of littoral prey availability.

Based on previous observations of species-specific migration patterns (Skov et al. 2008; Skov et al. 2011), prey fish were categorized as either potentially migratory, i.e. species that exhibit partial migration in open lakes (roach (*Rutilus rutilus*), bream (*Abramis brama* ≤ 30 cm), white bream (*Blicca bjoerkna* ≤ 30 cm), cyprinid hybrids), or as non-migratory prey fish species (eel (*Anguilla anguilla*), gudgeon (*Gobio gobio*), crucian carp (*Carassius carassius*), minnow (*Phoxinus phoxinus*), perch (*Perca fluviatilis*), pike (*Esox lucius*), rudd (*Scardinius erythrophthalmus*), ruffe (*Gymnocephalus cernua*), tench (*Tinca tinca*), three-spined stickleback (*Gasterosteus aculeatus*)). These groups of fish species are henceforth referred to as ‘potentially migratory’ and ‘non-migratory’ prey species, respectively, for both open and closed lakes.

Prey biomass and size

Pike stomach content samples were thawed in the laboratory and prey fish were identified to the lowest recognizable taxonomic level. Individual prey length (nearest mm, standard length) was

measured or estimated (if the prey fish was partly digested) using species-specific relationship between caudal fin and standard length (Table S2). These species-specific relationships were obtained from our electrofishing samples of fish used to estimate prey availability. Fresh weights of individual prey fish were then estimated from species-specific length-weight relationships, also obtained from the prey availability study (Table S2). Based on these we estimated total prey biomass as well as potentially migratory prey biomass per individual pike stomach. In addition, we calculated the mean prey biomass for each stomach to evaluate lake type variations in prey size in relation to migration period as we expected smaller mean prey sizes in lakes with partially migratory prey during the migration period.

Stable isotope analyses

Pike samples were prepared from white muscle tissue (216 ± 94 mg wet weight, mean \pm SD) taken anterior to the dorsal fin. All samples were dried at 55°C for 48 hours and homogenized using a TissueLyser II (QIAGEN[®]) grinder. Approximately 0.5 mg (dry mass) of sample (0.47 ± 0.03 mg, mean \pm SD) was weighed into pre-weighed tin capsules ($5 \cdot 9$ mm). Stable carbon isotope analyses were performed at the Swiss Federal Institute of Aquatic Science and Technology (Eawag), Center for Ecology, Evolution and Biogeochemistry (CEEB), Switzerland. Samples were combusted in a Flash 2000 elemental analyzer coupled to a Delta V Advantage isotope ratio mass spectrometer via a ConFlo IV interface. Standards for $\delta^{13}\text{C}$ were calibrated against Vienna Pee Dee Belemnite (VPDB).

We sampled mussels and pulmonate snails in each lake at the first and last sampling event. These samples, however, provided unreliable baselines over all sampling events. Instead, we tested for variation in size-specific patterns across populations (see below).

Statistical analyses

Prey availability

Prey data from transects were analyzed to test for seasonal differences in prey availability between lake type (open lakes and closed lakes) and prey type (potentially migratory species and non-migratory species). Seasons were defined as being outside (pre- and post-migratory period, i.e. time period 1 and 5) or inside (early, mid and late migratory period, i.e. time period 2, 3, and 4) the migratory period. Prior to analysis, total captured biomass from all transects in each sampling

session were summed and divided by total fishing time to obtain catch per unit effort (CPUE). The following mixed effects, random intercept model was fitted:

$$\begin{aligned} \text{Log}(\text{CPUE}_{ijkln}+1) &\sim N(\mu_{ijkln}, \sigma_{kl n}^2) \\ \mu_{ijkln} &= \alpha + \text{LT}_{ijkln} \cdot \text{PreyType}_{ijkln} \cdot \text{Season}_{ijkln} + a_j \\ a_j &\sim N(0, \sigma_a^2) \end{aligned} \tag{M1}$$

In this, observation i of log-transformed CPUE+1 from lake j being lake type (LT) k of prey type l sampled in season n is assumed to be normally distributed around μ_{ijkln} with variance $\sigma_{kl n}^2$, i.e. varying between combinations of k , l and n , thereby allowing for heterogeneity of variances. The random intercept a_j is normally distributed with mean zero and variance σ_a^2 and imposes a compound symmetry correlation structure allowing observations within each lake j to be correlated. A dummy variable coding the three-way interaction was used to obtain contrasts of interest (i.e. differences between seasons for combinations of prey type and lake type), by shifting the baseline. Additionally, we tested for differences between abundance of both resident and migratory prey types in open vs. closed lakes in the season defined as outside migration period. It should be noted when interpreting the results that sample size for this model was relatively low.

Diet

Since the majority of the pike (87.5%) had exclusively either potentially migratory- or non-migratory prey species in their diet, we translated proportion of potentially migratory prey in the diet into a binary variable “dominance of potentially migratory prey species”. Pike with an equal number of potentially migratory- and non-migratory prey species in the stomach (3.1% of all pike) were excluded from this analysis). We analysed dominance of potentially migratory prey species found in the stomachs of pike, using multinomial logistic regression with pike length, lake type, and sampling period (residence- vs. migration period (see below)) as explanatory variables. For simplicity, we did not include individual lake identity in our final analyses, as preliminary analyses showed no effect of individual lake.

We analysed total- and average biomass of prey fish (both log transformed) found in the stomachs of pike, using nested ANCOVA's. To reduce the number of interacting factors, we first ran analyses for different sampling periods (residence- and migration period) separately, testing for effects of pike size (length in mm), lake type (open versus closed), and individual lake identity nested under lake type. We subsequently ran analyses for each lake type separately to test for effects of pike size, sampling period, and lake identity, using ANCOVAs. Since stomach content gives a time-specific

indication of diet with little delay in the signal (unlike stable isotope analyses described below), we grouped the first and last sampling event (pre- and post-migration period) into a single descriptor, i.e. residence period. Similarly, we grouped the second to fourth sampling event (early-, mid- and late-migration period) into a single descriptor, migration period. Models were rerun without the lake type · pike size interaction term, in case this had a p-value above 0.1. When not specifically indicated in the results, interactions were non-significant and removed from models.

All analyses were carried out first for all prey species, and subsequently for potentially migratory prey species and for non-migratory prey species (see *Prey availability* section) separately.

Energy pathways

Unlike stomach content analyses that reflect current foraging, stable isotope ratios integrate foraging over several months, especially during winter (Thomas & Crowther 2015). Hence, differences between systems and individuals in stable isotope ratios should be interpreted as a result of recent rather than present differences in e.g. environmental conditions. For analyses of stable isotope ratios, we therefore chose seasonal contrast slightly differently from other analyses in the study, which investigates present differences (e.g. prey availability and stomach content).

Specifically, we only included the first sampling event, i.e. in the pre-migration period, in the residence period, and the following four periods in the migration period.

A nested analysis of variance (ANOVA), with lake identity nested under lake type, was fitted to test difference in relationship (slope) between length of pike and their stable carbon isotope signal between open and closed lakes and migration period.

Somatic condition of predators

A multilevel model with random intercept and slope was fitted to the data. The model imposes a compound symmetry correlation structure allowing observations within each lake to be correlated and allowing the length-weight relationship to vary between lakes. The following initial model was fitted

$$\begin{aligned} \text{Log}(W_{ij}) &\sim N(\mu_{ij}, \sigma^2) & (M2) \\ \mu_{ij} &= \alpha + \text{TP}_{ij} + \text{LT}_{ij} + \log(L_{ij}) + \text{TP}_{ij} \cdot \log(L_{ij}) + \text{LT}_{ij} \cdot \log(L_{ij}) + \text{TP}_{ij} \cdot \text{LT}_{ij} + a_j + b_j \cdot \\ &\log(L_{ij}) \\ a_j &\sim N(0, \sigma_a^2) \\ b_j &\sim N(0, \sigma_b^2) \end{aligned}$$

The model assumes that log-transformed weight of pike i from lake j is normally distributed with mean given by the predictor function μ_{ij} and variance σ^2 . The predictor function is specified as the summed effects of time period TP , lake type LT , log-transformed length $\log(L)$ and all two-way interactions between these, a common intercept α , lake-specific random intercept a and lake-specific random slope b . Both a and b are assumed to be normally distributed with mean zero and variances σ_a^2 and σ_b^2 , respectively. In addition to the initial model, models excluding each of the three two-way interactions were fitted. Model comparison and selection was based on deviance information criterion DIC. Comparison of population level differences in mean (log) weight between predators from the two different lake types and associated 50% and 90% credible intervals were obtained by sampling from the posterior distribution of model M2c (Table 2). Model fitting was performed in a MCMC-based Bayesian framework using JAGS (Plummer, 2003) and the R-package R2jags (Su & Yajima, 2015). This approach allowed calculations of e.g. period-specific population level differences in mean log(weight) between open and closed lakes and associated credible intervals by sampling the posterior distribution. Three Markov chains were used with 50,000 iterations each, a burn-in of 10,000 and a thinning rate of 10. A total of 12,000 iterations were thus used for the posterior distribution of each parameter. Non-informative normal priors were used for regression parameters and diffuse uniform priors (range 0 – 10) were used for the three variance parameters (σ^2 , σ_a^2 and σ_b^2).

Table 2: Summary of fitted models modelling log(Weight) as a function of common intercept (α), time period (TP), lake type (LT), log-transformed length ($\log(L)$) of pike (i) from lake (j), and relevant two-way interactions. The random component was identical in all models, namely $a_j + b_j \cdot \log(L_{ij})$. Blank spaces indicate which two-way interaction was taken out of models M2b, M2c, and M2d. Model M2c provided the parsimonious best fit and was used for subsequent analyses.

Model	Fixed part	DIC	Δ DIC
M2a	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + TP_{ij} \cdot \log(L_{ij}) + LT_{ij} \cdot \log(L_{ij}) + TP_{ij} \cdot LT_{ij}$	-1051.3	-
M2b	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + LT_{ij} \cdot \log(L_{ij}) + TP_{ij} \cdot LT_{ij}$	-1036.7	14.6
M2c	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + TP_{ij} \cdot \log(L_{ij}) + TP_{ij} \cdot LT_{ij}$	-1052.1	-0.8
M2d	$\alpha + TP_{ij} + LT_{ij} + \log(L_{ij}) + TP_{ij} \cdot \log(L_{ij}) + LT_{ij} \cdot \log(L_{ij})$	-1047.0	4.3

Statistical analyses of prey availability and somatic condition were carried out in R (R Development Core Team 2016) and analyses of biomass and size of ingested prey and energy pathways in SPSS, v. 23.0. (SPSS Inc., Chicago, IL, USA).

Results

Prey fish availability and community structure

The biomass of potentially migratory prey present in the lake was significantly lower during the migration period in open lakes ($p < 0.001$; Fig. 1, Table 3), whereas in closed lakes the abundance of potentially migratory prey species did not differ with season ($p = 0.96$; Fig. 1, Table 3).

Likewise, the abundance of non-migratory prey did not decrease significantly during the migration period; no significant difference in biomass was found between periods in either of the two lake types ($p > 0.10$; Fig. 1, Table 2).

During the residence period, we found a significantly higher abundance of potentially migratory prey species in the open lakes than in the closed lakes (Est. Diff. (s.e.) = 1.59 (0.63), $p = 0.0145$).

For non-migratory prey species, no such difference was found (Est. Diff (s.e.) = 0.14 (0.47), p -value=0.76).

Table 3: Estimated differences in prey availability between inside vs. outside migration period for all four combinations of lake type and prey type obtained from the linear mixed effects model (M1). Only the combination of open lake type and migratory prey (d) had significantly different prey availability between seasons. Compare with figure 1.

	Lake type	Prey type	Est. Diff. (s.e.)	p-value
(a)	Closed	Resident	0.88 (0.55)	0.11
(b)	Open	Resident	0.81 (0.61)	0.19
(c)	Closed	Migratory	0.03 (0.65)	0.96
(d)	Open	Migratory	2.23 (0.45)	<0.0001

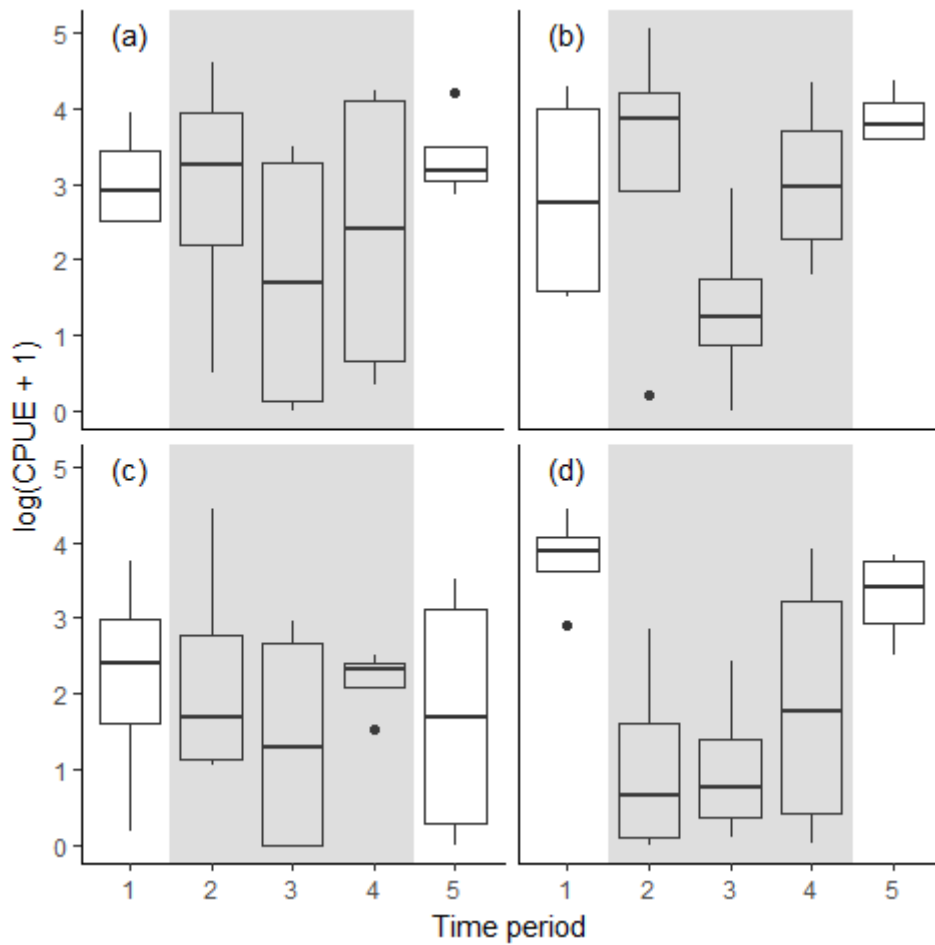


Figure 1: Prey availability measured as $\log(\text{CPUE} + 1)$ in the four combinations of lake type and prey type. Top row represent resident prey type, bottom row migratory prey type while left and right columns represent closed and open lake types, respectively (compare with Table 2). Shaded areas represent the migration periods. There was significantly higher prey availability outside than inside the migration period in migratory prey in open lakes ($p < 0.0001$, panel (d); Table 2).

Diet: Relative contribution of potentially migratory prey species

The diet of pike, all lakes combined, was as expected numerically dominated by fish (93%) whereas small invertebrates (6%) and plant material (1%) only made up a minor proportion of the diet. Of the prey identified to species level ($n=879$), there was a strong dominance of roach (71.3%), followed by perch (9.4%) and bream (8.4%). During the entire sampling period, potentially migratory prey species were more abundant in the diet than non-migratory prey and accounted numerically for 85% of the prey fish in the diet. Overall, there was a significant effect of both pike size (multinomial logistic regression; $\chi^2_{1,288} = 5.58$; $p = 0.018$) and time period (migratory vs. residence period; multinomial logistic regression; $\chi^2_{1,288} = 21.3$; $p < 0.001$) on the dominance of potentially migratory prey species in the pike diet. Specifically, potentially migratory prey species

were more frequent in the diet of larger pike and during the winter migration period (Fig. 2). Lake type did not have any significant effect on the dominance of potentially migratory prey species in the diet (multinomial logistic regression; $\chi^2_{1,288} = 0.97$; $p = 0.33$).

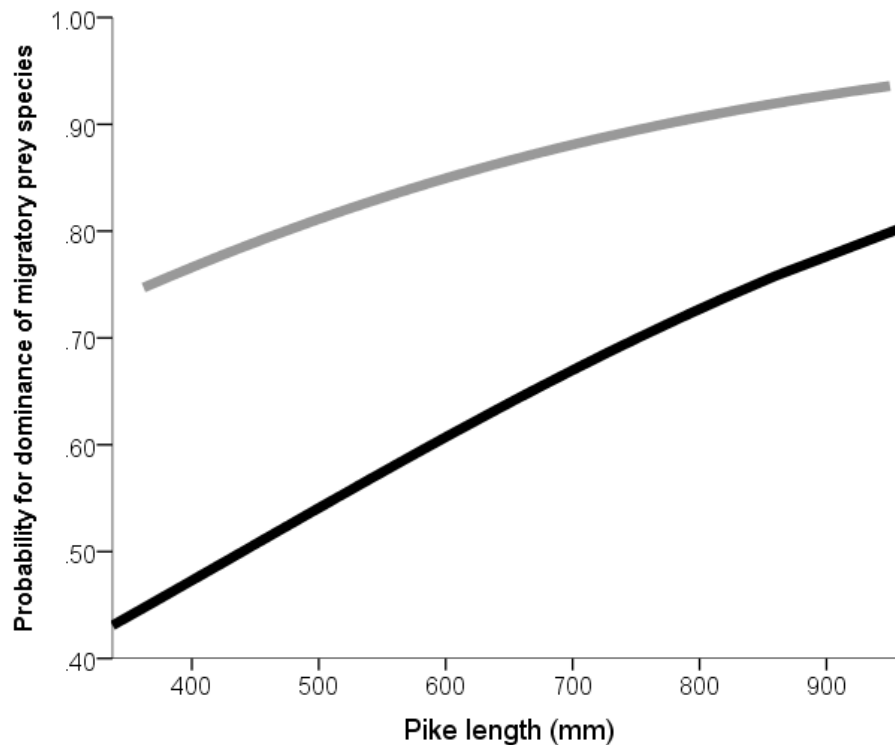


Figure 2: Estimated probabilities for dominance of potentially migratory prey species in the diet of pike as a function of pike length and time period (prey residence period: black line; prey migratory period: grey line). Potential migratory prey fish species include roach, bream (≤ 30 cm), white bream (≤ 30 cm), cyprinid) and non-migratory prey fish species include eel, crucian carp, perch, pike, rudd, ruffe, three-spined stickleback.

Diet: Total biomass of ingested prey

During the migration period, the total estimated biomass (log-transformed) of fish in the stomachs increased with pike size (nested ANCOVA; $F_{1,155} = 11.0$; $p = 0.001$) and differed significantly between lake types (nested ANCOVA; $F_{1,155} = 4.43$; $p = 0.037$), with pike in closed lakes generally having a higher biomass of fish in the stomachs (Fig. 3B). During the residence period, there was only a significant effect of size (nested ANCOVA; $F_{1,81} = 5.68$; $p = 0.020$), but not of lake type (nested ANCOVA; $F_{1,81} = 0.14$; $p = 0.710$; Fig. 3A). There was no effect of lake identity (nested ANCOVA; $F_{6,155} = 0.53$; $p = 0.224$ and nested ANCOVA; $F_{6,81} = 2.01$; $p = 0.075$ for migration- and residence period, respectively) and the interaction term between lake type and pike length was also non-significant (nested ANCOVA; $F_{1,155} = 0.20$; $p = 0.447$ and nested ANCOVA; $F_{1,81} = 0.03$; $p = 0.776$ for migration- and residence period, respectively).

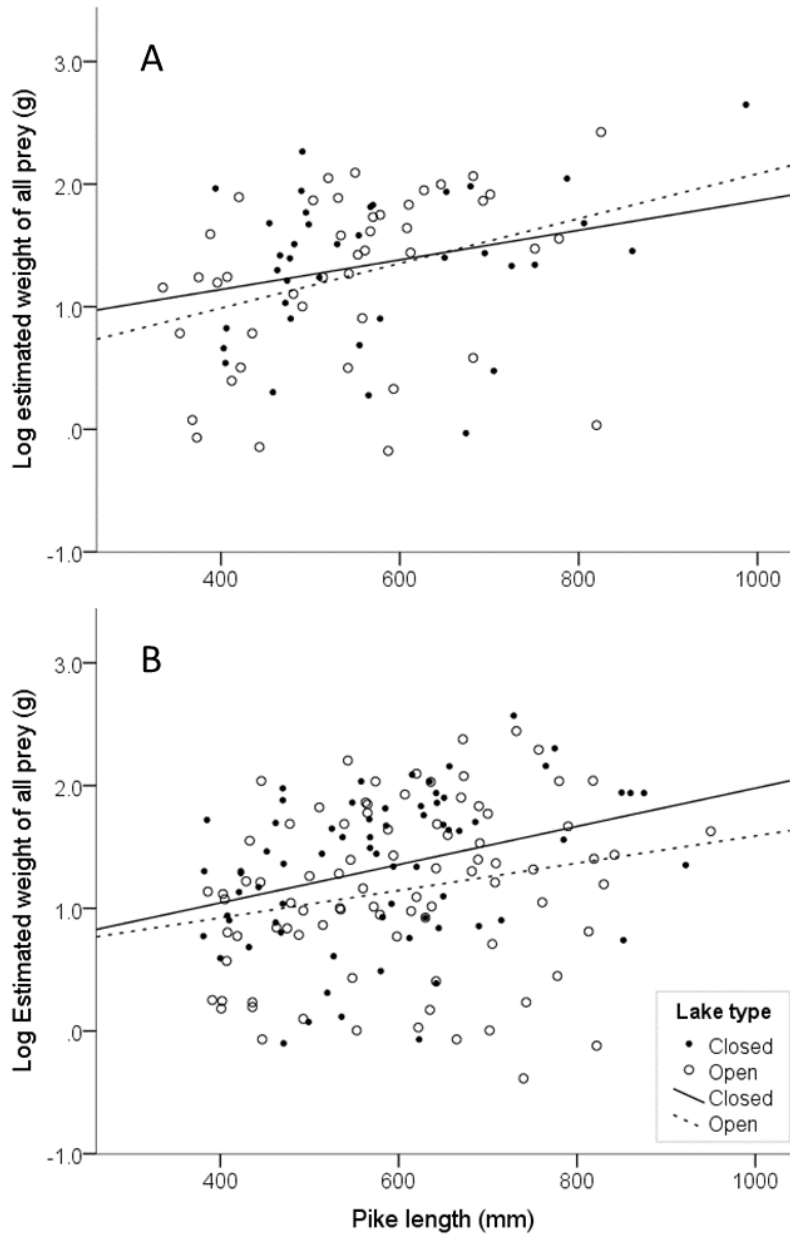


Figure 3: Total estimated weight of prey fish in pike stomachs in the residence (A) and migratory period (B) in open (open circles, broken line) and closed lakes (filled circles and full line) as a function of individual pike length.

We found the same pattern when only considering potentially migratory prey species, i.e. a positive effect of pike size (nested ANCOVA; $F_{1,133} = 10.2$; $p = 0.002$) and a higher biomass in the stomachs in closed lakes (nested ANCOVA; $F_{1,133} = 6.22$; $p = 0.014$) during the migration period (Fig. S1B), and only an effect of pike size (nested ANCOVA; $F_{1,49} = 5.49$; $p = 0.024$) but not of lake type (nested ANCOVA; $F_{1,49} = 0.39$; $p = 0.537$) during the residence period (Fig. S1A). Here, however, there was a lake identity effect for both the migration (nested ANCOVA; $F_{6,133} = 2.22$; $p = 0.045$) and the residence period (nested ANCOVA; $F_{6,49} = 2.69$; $p = 0.027$). For total biomass of non-migratory prey species in the stomachs of pike, there were no effect of neither pike length (nested ANCOVA; $F_{1,38} = 0.49$; $p = 0.49$ and nested ANCOVA; $F_{1,37} < 0.01$; $p = 0.999$ in the migratory and

residence periods, respectively; Fig. S1C & S1D), nor lake type (nested ANCOVA; $F_{1,38} = 0.01$; $p = 0.92$ and nested ANCOVA; $F_{1,37} = 0.02$; $p = 0.89$ in the migratory and residence periods, respectively). Here, there was a lake identity effect only in the migratory period (nested ANCOVA; $F_{6,38} = 4.00$; $p = 0.005$ and nested ANCOVA; $F_{6,37} = 1.62$; $p = 0.178$ in the migratory and residence periods, respectively).

Diet: Size of ingested prey fish

Generally, over the whole year and across lake types, the average biomass of individual prey fish found in the stomachs of pike increased with pike size (Fig. 4). After taking this into consideration, pike in open lakes had significantly smaller prey in their stomachs than pike in closed lakes during the migration period (nested ANCOVA; size: $F_{1,155} = 4.22$; $p = 0.042$; lake type: $F_{1,155} = 12.6$; $p = 0.001$, Fig. 4B) and, in addition, there was a lake identity effect (nested ANCOVA; $F_{6,155} = 3.70$; $p = 0.002$). During the residence period, the effect of pike length was marginally significant (nested ANCOVA; $F_{1,81} = 3.66$; $p = 0.060$), but there were no effects of lake type (nested ANCOVA; $F_{1,81} = 0.30$; $p = 0.583$) or lake identity (nested ANCOVA; $F_{6,81} = 1.73$; $p = 0.127$) on the average size of prey found in the individual pike stomachs (Fig. 4A).

Similar to total biomass in the stomachs, we found a highly significant effect of lake type on average size of prey during the migration period, when only considering potentially migratory prey species (nested ANCOVA; lake type: $F_{1,133} = 19.2$; $p < 0.001$; size: $F_{1,133} = 7.40$; $p = 0.007$; lake: $F_{6,133} = 4.33$; $p = 0.001$; Fig. S2B). However, during the residence period, no such effect was found (nested ANCOVA; lake type: $F_{1,49} = 0.11$; $p = 0.746$; size: $F_{1,49} = 3.48$; $p = 0.069$; lake: $F_{6,49} = 2.50$; $p = 0.038$; Fig. S2A). For non-migratory prey species, there was no effect of lake type neither in the migration period (nested ANCOVA; lake type: $F_{1,38} = 0.05$; $p = 0.83$; size: $F_{1,38} = 0.57$; $p = 0.46$; lake: $F_{6,38} = 4.36$; $p = 0.003$; Fig. S2D), nor in the residence period (lake type: $F_{1,37} < 0.01$; $p = 0.98$; size: $F_{1,37} = 0.01$; $p = 0.93$; lake: $F_{6,37} = 1.87$; $p = 0.122$; Fig. S2C).

When contrasting within lake types between time periods, we found a significant effect of time period on average size of prey in both open lakes (ANCOVA; time period: $F_{1,130} = 12.6$; $p < 0.001$; size: $F_{1,130} = 4.23$; $p = 0.042$; lake: $F_{3,130} = 0.60$; $p = 0.62$), and closed lakes (ANCOVA; time period: $F_{1,106} = 4.78$; $p = 0.031$; size: $F_{1,106} = 6.02$; $p = 0.016$; lake: $F_{3,106} = 7.19$; $p < 0.001$). Specifically, pike generally fed on smaller prey during winter, and this was more pronounced in open lakes. Similarly, we found a highly significant difference in size of potentially migratory prey species in the stomachs of pike between the residence- and migration periods in open lakes

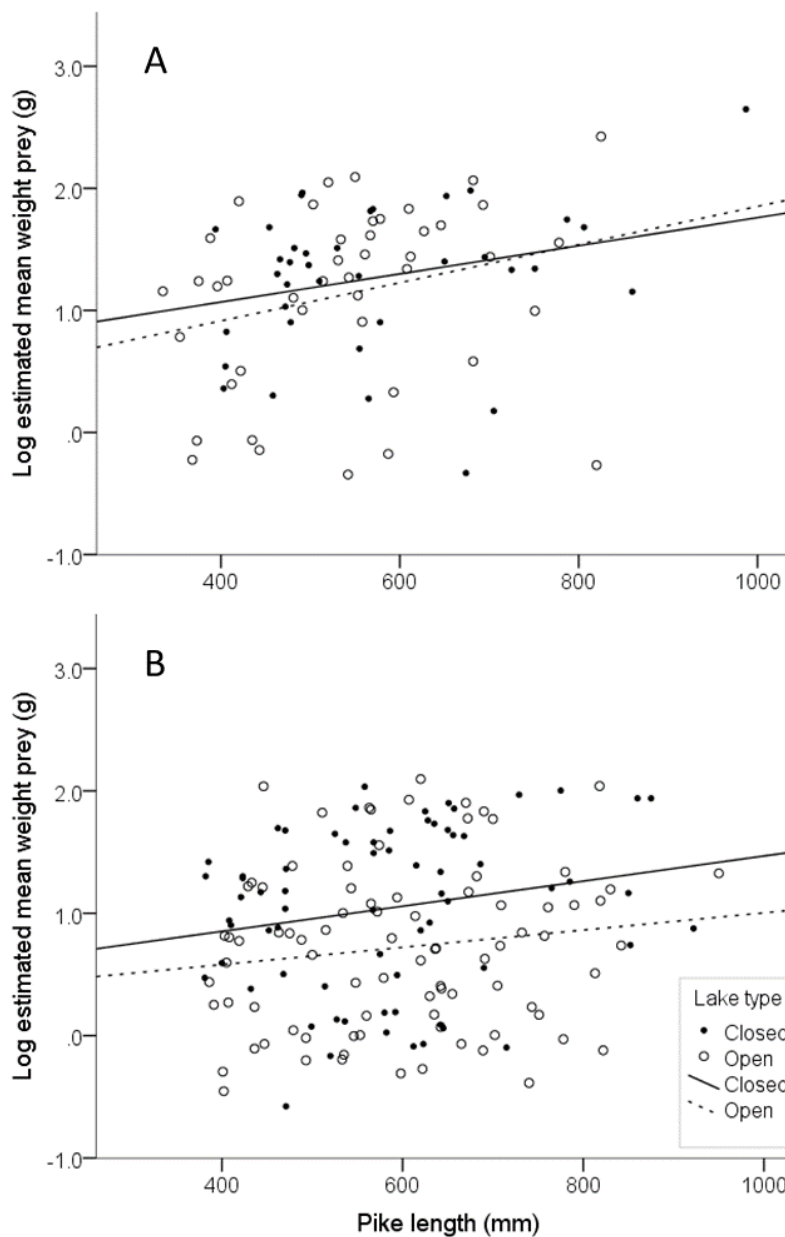


Figure 4: Mean estimated weight (log transformed) of individual prey fish in pike stomachs in the residence (A) and migratory period (B) in open (open circles, broken line) and closed lakes (filled circles and full line) as a function of individual pike length.

(ANCOVA; lake type: $F_{1,102} = 15.5$; $p < 0.001$; size: $F_{1,102} = 3.78$; $p = 0.055$; lake: $F_{3,102} = 2.52$; $p = 0.062$), but not in closed lakes (ANCOVA; lake type: $F_{1,80} = 0.44$; $p = 0.51$; size: $F_{1,80} = 11.1$; $p = 0.001$; lake: $F_{3,80} = 10.1$; $p < 0.001$). In the closed lakes, the average weight of resident prey species in the diet of the pike were significantly lower during the winter migration period (ANCOVA; $F_{1,36} = 4.78$; $p = 0.037$), but we found no effect of either pike length (ANCOVA; $F_{1,36} = 0.15$; $p = 0.70$) or lake identity (ANCOVA; $F_{3,36} = 2.05$; $p = 0.13$).

In the open lakes, there were no significant relationship between average weight of non-migratory prey species in the diet and time period (ANCOVA; $F_{1,39} = 0.88$; $p = 0.35$) and, further, no effect of size (ANCOVA; $F_{1,39} = 0.73$; $p = 0.40$). Here, however, we found a significant effect of individual lake identity (ANCOVA; $F_{3,39} = 6.56$; $p = 0.001$).

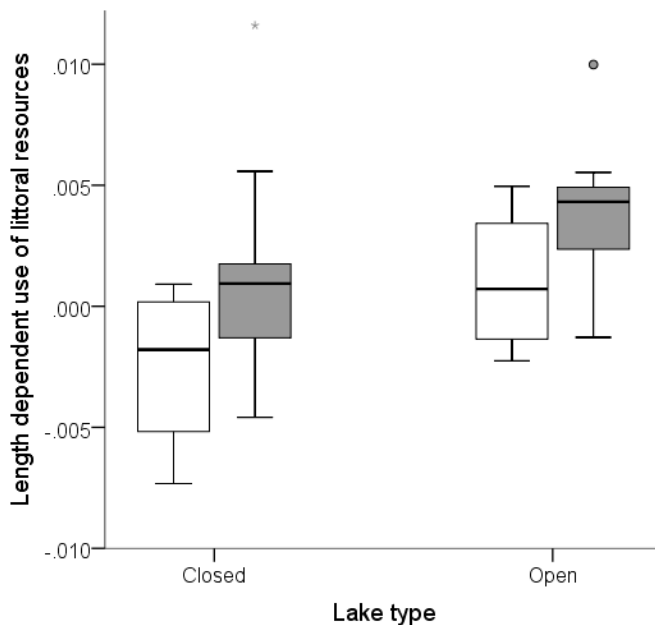


Figure 5: Difference in length dependent use of littoral resources, obtained from regression slope between pike $\delta^{13}\text{C}$ -isotope values and length, between closed and open lakes with a contrast between sampling periods (white boxes: pre-migration period; shaded boxes: post-migration period). The length dependent use of littoral resources is higher in open lakes in the migration period as compared to closed lakes in general and open lakes before the migration period.

Energy pathways

The size-dependent use of littoral resources (Fig. S3) was significantly influenced both by lake type (nested ANOVA; $F_{1,39} = 14.6$; $p = 0.001$; Fig. 5) and by sampling period (residence vs. migration period; $F_{1,39} = 9.0$; $p = 0.005$), with an additional effect of lake identity ($F_{6,39} = 4.3$; $p = 0.003$; Fig. 5). When analyzing residence and migration periods separately, we found a significant effect of lake type during the migration period (nested ANOVA; $F_{1,31} = 10.4$; $p = 0.004$), but not in the residence period (ANOVA; $F_{1,6} = 2.2$; $p = 0.19$). When analyzing lake types separately, we found a significant effect of migration period in open lakes (ANOVA; $F_{1,19} = 5.1$; $p = 0.040$), but not in closed lakes (ANOVA; $F_{1,20} = 4.02$; $p = 0.063$). Specifically, the positive effect of pike length on

relative dependence on littoral resources was more pronounced in open lakes during the migration period.

Somatic condition of predators

The effect of time period on the weight-length relationship of pike varied with both pike length (Table 2, M2b; $\Delta\text{DIC} = 14.6$) and lake type (Table 2, M2d; $\Delta\text{DIC} = 4.3$). Conversely, the weight-length relationship was found to be practically identical in both lake types (Table 2, M2c: $\Delta\text{DIC} = -0.8$). Thus, model M2c provided the best parsimonious fit and was used for subsequent comparisons to elucidate the interplay between lake type and time period and associated effect on pike somatic condition, i.e. the important interaction between lake type and time period ($\Delta\text{DIC} = 4.3$). Mean somatic condition of the predators in lakes with partially migratory prey was lower before the migration period (pre-migration period), increased during the migration period (early-, mid- and late-migration periods) and decreased again after the migration period (post-migration period) (Fig. 6).

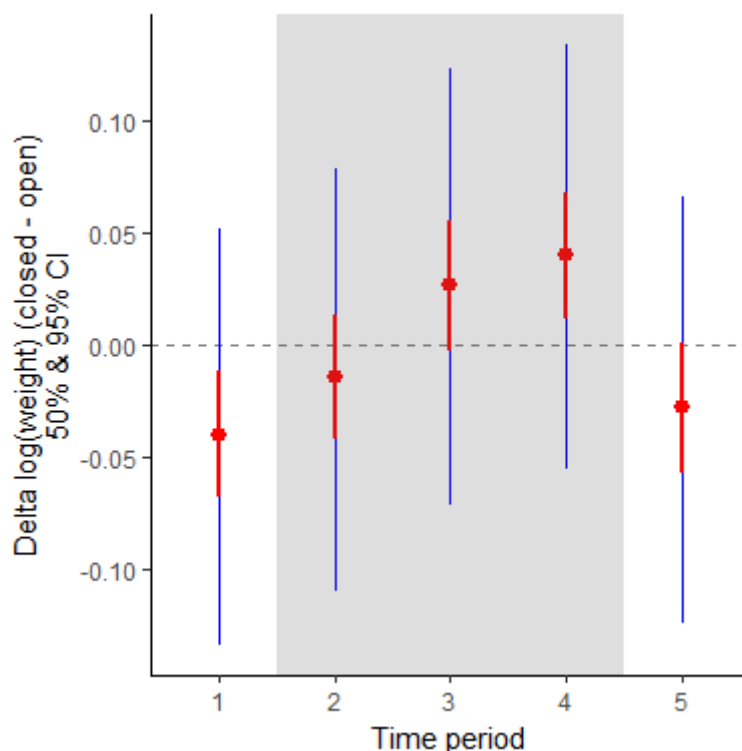


Figure 6: Mean somatic condition of pike in open lakes declined during the migration period and was 4 % lower at the end of the migration period (period 4) compared to pike in closed lakes, i.e. lakes without prey seasonal partial migration. Differences in population level mean (log) weight between pike in open and closed lakes and associated 50 % and 90 % credible intervals were obtained by sampling from the posterior distribution of model M2c.

Discussion

In recent years, there has been an increasing recognition that migration can have profound ecological consequences through changes in predator-prey interactions (Post et al. 2008; Brodersen et al. 2011a), yet empirical demonstrations remain scarce. Previous studies on how migratory prey may influence resident predators have generally focused on how migration can lead to a temporary super-abundance of food for resident predators upon arrival of migratory prey (Hilderbrand et al. 1996; Samelius et al. 2011; Bauer & Hoyer 2014 and references therein). In comparison, much less focus has been paid to the loss of potential foraging opportunities for resident predators when their prey leaves during the seasonal migrations. Our study reveals that seasonal migration of prey can have multiple effects on predator foraging ecology and seasonally change the relative importance of alternative energy pathways in lake ecosystems. Migration may also have implications for predator fitness, as suggested by reduced somatic condition of predators in lakes with prey migration towards the end of the prey migration period.

Due to the scarcity of systems that have either migratory or non-migratory prey populations of the same species and difficulties with replication at the ecosystem level, it is difficult to quantify and partition the effect of migration from those of seasonality. In the present study, we took advantage of a set of replicated lakes, that allow or constrain seasonal migration in a prey species, to quantify the effects of prey migration on the feeding ecology of a top predator. First, we found that overall prey availability in open lake ecosystems is reduced during the migration period, as expected from earlier findings on prey fish migration patterns (e.g. Skov et al. 2008). Second, we found that total biomass of prey ingested by the pike is reduced during the migration period in open lakes and also lower than in closed lakes during this period. This difference is driven by a specific reduction in the biomass of potentially migratory prey species in the pike diet in the open lakes during the winter migration period. This suggests that prey migration causes, first, a reduction in prey availability and, second, a reduction in ingested prey biomass by the predators in the system. In terrestrial ecosystems, similar seasonal changes in foraging patterns have been seen in resident predators as a response to ungulate prey migration (e.g. Owen-Smith 2008; Sand et al. 2008; Metz et al. 2012; Elbroch et al. 2013). For example, Fryxell and colleagues (2007) estimated that wildebeest (*Connochaetes taurinus*) migration out of lion (*Panthera leo*) territories reduces lion daily average feeding rates on wildebeest by 82%. However, empirical evidence including replication and negative controls has hitherto been lacking.

We additionally found that the mean size of prey ingested by pike is reduced during the migration period in open lakes and is lower than in the closed lakes during this period. This is likely caused by a general body size effect on propensity to migrate in roach, the main prey species, where smaller individuals generally have a lower migratory propensity than larger fish (Brodersen et al. 2008b), resulting in small individuals being more abundant in the lake during the migratory period.

Migration-induced seasonal changes in relative density of different types of prey have the potential to alter energy pathways within lakes between seasons. Several lines of evidence suggest that migratory and resident prey may differ in their position in the food web, i.e. in their relative reliance on littoral vs. pelagic food chains. Prey fish species associated with the open water habitat are generally more migratory than prey species associated with the structurally complex littoral habitat (Skov et al. 2008). The primary prey species in this study, roach, generally has an ontogenetic niche shift from planktivory at smaller sizes towards an inclusion of a higher proportion of benthic macroinvertebrates in larger individuals (Hjelm et al. 2003), and, further, roach increases migratory propensity with size in our study system (Brodersen et al. 2008b). Lastly, roach populations consist of different phenotypes, with deep-bodied individuals being mainly resident and slender bodied individuals being migratory (Chapman et al. 2015). These phenotypes are generally recognized as littoral and pelagic specialists, respectively (Faulks et al. 2015). This suggests that prey fish remaining in the lakes during the migratory period would be more dependent on littoral resources than the migratory prey fish.

In accordance with the stomach content analyses, we found strong support for a predator size-dependent response in reliance on littoral resources during the migration period in lakes with prey migration, with larger pike having a relatively higher reliance on littoral energy pathways than smaller pike, specifically during the migration period and only in lakes with partially migratory prey. We suggest that this change is caused by a seasonal shift in available prey types primarily affecting large predators in open lakes, through a reduction in large open-water prey fish, i.e. prey with a relatively high dependence on pelagic resources, during the migration period. Top predators, here represented by pike, are important integrators of different energy pathways in ecosystems (Vander Zanden & Vadeboncoeur 2002). The observed lake-type specific seasonal change in relative littoral dependence of the dominant top predator indicates a change in energy pathways in the lake food web caused by partial migration of prey. Our study, hence, illustrates that migration of

prey can change the relative importance of different energy pathways from primary producers to top predators, when the foraging ecology of resident prey differs from that of migratory prey.

In combination, our results suggest that predator foraging regimes temporally change due to migration of a large fraction of especially larger individuals of the prey community. Aligned with our prediction, predators in open lakes had reduced somatic condition, especially towards the end of the migration period, potentially as a consequence of an overall lower food intake or foraging on smaller prey containing less energy per weight than larger prey, e.g. due to relatively lower lipid content (e.g. Thompson et al. 1991). Since body condition integrates previous feeding conditions, it is not surprising that predator body condition differences become apparent at the end of the migration period, although tendencies toward a reduced body condition of pike in open lakes could be noted already during the mid-migration period. Interestingly, after the migration period has ended, i.e. when prey fish had returned from the streams to the lake habitat, the difference in somatic condition between the predators in the different lake types could no longer be detected. This is likely a result of compensatory feeding in the predators upon return of large numbers of migrating prey.

Reduced somatic condition can be considered as a fitness cost for animals, e.g. due to reduced reproductive success and resistance to diseases (Huntingford et al. 2006; Araki et al. 2009). In our study, the maximum difference in somatic condition occurred shortly before reproduction, which may suggest an influence on reproductive output. Although a 4% reduction in condition may seem minor, it is important to consider that fish tend to compensate somatic energy loss with increased water content (e.g. Brodersen et al. 2011b), i.e. somatic condition estimates based on wet weight are conservative estimates of reduced energy content. Hence, our study demonstrates that migrating prey can potentially have important fitness implications for resident predators.

A crucial question in migration biology is whether prey migration affects overall population size and relative dominance in the community of the potentially migratory species. We found that abundance of potentially migratory prey species during the lake residence period in summer is higher in lakes where the prey can migrate as compared to lakes where the prey are restricted to year round residence. Hence, potentially migratory species appear to have a relative competitive advantage in systems where they are able to reduce their predation rate in winter, by migration into refuges in streams. It is interesting in this regard that the effect of season on the relative

contribution of potentially migratory prey species to the diet of predatory pike was more pronounced than the effect of migratory opportunity, suggesting that the potentially migratory prey species are particularly vulnerable during winter, which also may explain why some prey species are more migratory than others.

Conclusions

Previous studies have focused on top-down effects of migratory fish (Brodersen et al. 2011a; Post et al. 2008) or on bottom-up effects mediated by nutrient transfer between ecosystems by migratory animals (Holtgrieve & Schindler 2011; Subalusky et al. 2017). However, based on our results we conclude that partially migratory fish are also causing bottom-up effects on resident predators, change energy pathways through the food web and alter community structure of prey. The spatial replication of lake ecosystems offers a unique design with separate predator-prey systems as replicated experimental units. Such replication may be difficult to obtain in terrestrial or marine ecosystems, but multiple solitary observations from different terrestrial ecosystems suggest that such bottom-up trophic effects may be widespread.

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Supplementary material

Table S1. Pike sampled in eight lakes at five sampling periods. For each sampling date in each lake mean length (total length, mm), mean weight (g), number (N) of pike caught, and percent empty stomachs are listed. ¹⁾ indicate one pike were the stomach was not pumped and ²⁾ indicate two pike that were not weighed (Table S1 is illustrated on page 94-96).

Lake	Lake type	Sampling date	Migration period	Size interval (mm); mean length (mm \pm SE)	Mean weight (g \pm SE)	N	Empty stomachs (%)
Fjällfotasjön	Closed	9/1/2011	Pre-migration	358-981; 508.6 \pm 36.5	1083.5 \pm 305.7	20	70
Fjällfotasjön	Closed	11/9/2011	Early migration	362-592; 458.5 \pm 14.5	624.1 \pm 72.6	17	53
Fjällfotasjön	Closed	1/18/2012	Mid-migration	392-662; 498.4 \pm 23.1	870 \pm 130.4	11	55
Fjällfotasjön	Closed	3/23/2012	Late migration	361-669; 520.7 \pm 28.6	1015 \pm 174.7	12	75
Fjällfotasjön	Closed	5/16/2012	Post migration	355-553; 473.6 \pm 11.1	682.5 \pm 51.4	20	60
Halesø	Closed	8/24+26/2011	Pre-migration	463-689; 545.5 \pm 17.6	1003.1 \pm 95.8	13	77
Halesø	Closed	11/11/2011	Early migration	382-812; 574.6 \pm 27	1278.9 \pm 183.8	18	61
Halesø	Closed	1/19/2012	Mid-migration	420-713; 555.1 \pm 23.2	1171.4 \pm 140.5	14	31 ¹⁾
Halesø	Closed	3/19/2012	Late migration	385-680; 556.5 \pm 22.4	1233.8 \pm 129.9	13	8
Halesø	Closed	5/16/2012	Post migration	510-791; 643.3 \pm 19.3	1664.7 \pm 131	17	47
Havgårdssjön	Closed	8/30/2011	Pre-migration	458-1017; 640.8 \pm 35.6	1832.1 \pm 329.8	19	53
Havgårdssjön	Closed	11/10/2011	Early migration	471-922; 659.7 \pm 25.6	2010.5 \pm 237.8	19	11
Havgårdssjön	Closed	1/19/2012	Mid-migration	357-939; 585.3 \pm 37.7	1705 \pm 339.8	20	80
Havgårdssjön	Closed	3/27/2012	Late migration	372-875; 550.3 \pm 32.8	1283.9 \pm 266.2 ²⁾	20	45
Havgårdssjön	Closed	5/16/2012	Post migration	381-860; 627.9 \pm 32.5	1848 \pm 268	20	70
Udbyover	Closed	8/1/2011	Pre-migration	455-850; 682.6 \pm 31.5	1848 \pm 268	14	50

Lake	Lake type	Sampling date	Migration period	Size interval (mm); mean length (mm \pm SE)	Mean weight (g \pm SE)	N	Empty stomachs (%)
Udbyover	Closed	11/21/2011	Early migration	351-860; 643.4 \pm 29.7	2265 \pm 300.9	18	33
Udbyover	Closed	3/5/2012	Mid-migration	508-842; 671.8 \pm 27	2746.4 \pm 349.7	14	71
Udbyover	Closed	3/20/2012	Late migration	398-790; 632.8 \pm 27.8	2097.9 \pm 268.6	19	63
Udbyover	Closed	5/24/2012	Post migration	490-845; 644.3 \pm 27.4	2169.3 \pm 265.6	15	87
Krankesjön	Open	8/18/2011	Pre-migration	380-838; 618 \pm 28	1686.9 \pm 220.3	24	67
Krankesjön	Open	11/7/2011	Early migration	368-818; 633.3 \pm 31.9	1835.7 \pm 245.1	21	48
Krankesjön	Open	1/17/2012	Mid-migration	544-830; 693.8 \pm 33.6	2320 \pm 324.3	9	44
Krankesjön	Open	3/29/2012	Late migration	359-813; 615.5 \pm 32.5	1755.5 \pm 231	20	55
Krankesjön	Open	5/14/2012	Post migration	373-813; 586.6 \pm 36.7	1546.1 \pm 261	18	61
Loldrup	Open	8/26+9/12+13/2011	Pre-migration	335-825; 552.9 \pm 32.3	1291.5 \pm 200.9	17	35
Loldrup	Open	11/16/2011	Early migration	419-839; 672.1 \pm 31.7	2382.1 \pm 322	14	29
Loldrup	Open	2/28/2012	Mid-migration	429-822; 621.9 \pm 38.3	2063.8 \pm 369.6	13	15
Loldrup	Open	3/21+29/2012	Late migration	385-746; 517.6 \pm 52.4	997.5 \pm 270.3	8	25
Loldrup	Open	5/15/2012	Post migration	407-800; 578.5 \pm 41.1	1449 \pm 307.1	10	40
Stigsholm	Open	8/25/2011	Pre-migration	368-778; 559.7 \pm 31.8	1281.8 \pm 201.8	18	33
Stigsholm	Open	11/17/2011	Early-migration	436-1010; 627.7 \pm 35.4	2014.5 \pm 435.4	20	55

Lake	Lake type	Sampling date	Migration period	Size interval (mm); mean length (mm \pm SE)	Mean weight (g \pm SE)	N	Empty stomachs (%)
Stigsholm	Open	1/18/2012	Mid-migration	408-950; 604.8 \pm 33.2	1662.5 \pm 343	16	6
Stigsholm	Open	3/29/2012	Late migration	408-761; 547.8 \pm 26.3	1180.6 \pm 185.3	17	35
Stigsholm	Open	5/14/2012	Post migration	420-800; 577.7 \pm 27.1	1352.5 \pm 170.1	16	25
Søgård	Open	8/23/2011	Pre-migration	354-855; 614.9 \pm 49.8	1802 \pm 352.8	10	40
Søgård	Open	11/24/2011	Early migration	407-995; 569.2 \pm 43.8	1485.4 \pm 358.7	13	23
Søgård	Open	3/6/2012	Mid-migration	386-739; 480.9 \pm 49.5	954.3 \pm 389	7	14
Søgård	Open	3/22/2012	Late migration	402-700; 519.6 \pm 31	1100.8 \pm 221.9	12	0
Søgård	Open	5/23/2012	Post migration	402-700; 519.6 \pm 31	1333.6 \pm 279.6	11	64

Table S2. Species-specific length-weight relationships obtained from prey availability study. Number in () next to species name is number of fish used to estimate the relationships. Parameters used is standard length (SL), total length (TL), caudal fin length (CF), body depth (BD) all measured in mm and weight (W) measured in g.

	Roach (4966)	Bream (158)	White bream (16)	Perch (1402)	Pike (23)	Three-spined stickleback (21)
Standard length	$3.57 \cdot CF + 4.87$ $R^2=0.96$	$3.04 \cdot CF + 3.73$ $R^2=0.92$	$2.87 \cdot CF + 11.84$ $R^2=0.96$	$4.36 \cdot CF + 11.26$ $R^2=0.79$	$4.52 \cdot CF + 46.80$ $R^2=0.75$	
Standard length	$0.79 \cdot TL + 0.66$ $R^2=1.00$	$0.76 \cdot TL - 0.17$ $R^2=1.00$	$0.75 \cdot TL + 2.38$ $R^2=1.00$	$0.83 \cdot TL + 0.71$ $R^2=0.98$	$0.85 \cdot TL + 0.60$ $R^2=0.99$	$0.76 \cdot TL + 4.69$ $R^2=0.99$
Standard length	$40.80 \cdot W^{0.30}$ $R^2=0.99$					
Weight	$4 \cdot 10^6 \cdot SL^{3.35}$ $R^2=0.99$	$5 \cdot 10^6 \cdot SL^{3.32}$ $R^2=0.99$	$2 \cdot 10^5 \cdot SL^{3.07}$ $R^2=0.97$	$8 \cdot 10^6 \cdot SL^{3.21}$ $R^2=0.98$	$1 \cdot 10^5 \cdot SL^{2.95}$ $R^2=0.89$	
Weight	$4 \cdot 10^6 \cdot TL^{3.16}$ $R^2=0.98$	$2 \cdot 10^6 \cdot TL^{3.31}$ $R^2=0.99$	$1 \cdot 10^5 \cdot TL^{3.02}$ $R^2=0.98$	$8 \cdot 10^6 \cdot TL^{3.07}$ $R^2=0.94$	$9 \cdot 10^6 \cdot TL^{2.95}$ $R^2=0.89$	
Body depth	$0.34 \cdot SL - 4.04$ $R^2=0.98$	$0.46 \cdot SL - 9.95$ $R^2=0.97$	$0.43 \cdot SL - 6.18$ $R^2=0.99$	$0.33 \cdot SL - 3.05$ $R^2=0.96$	$0.17 \cdot SL + 2.70$ $R^2=0.85$	
Body depth	$0.27 \cdot TL - 3.78$ $R^2=0.98$	$0.35 \cdot TL - 10.54$ $R^2=0.97$	$0.32 \cdot TL - 5.20$ $R^2=0.99$	$0.28 \cdot TL - 3.41$ $R^2=0.97$	$0.14 \cdot TL + 3.09$ $R^2=0.86$	

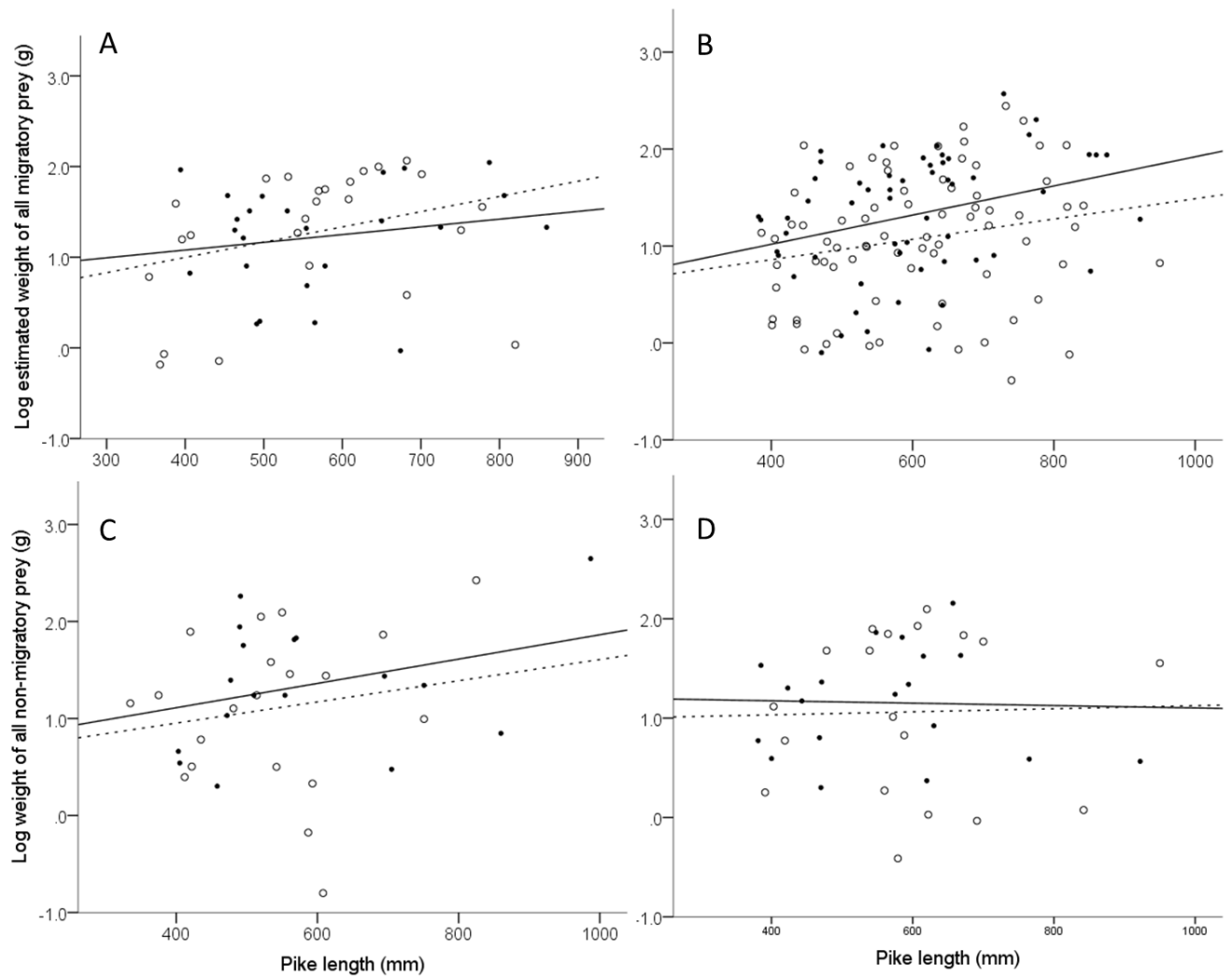


Figure S1: Total estimated weight of migratory (A & B) and non-migratory prey fish (C & D) in pike stomachs in the residence (A & C) and migratory period (B & D) in open (open circles, broken line) and closed lakes (filled circles and full line) as a function of individual pike length.

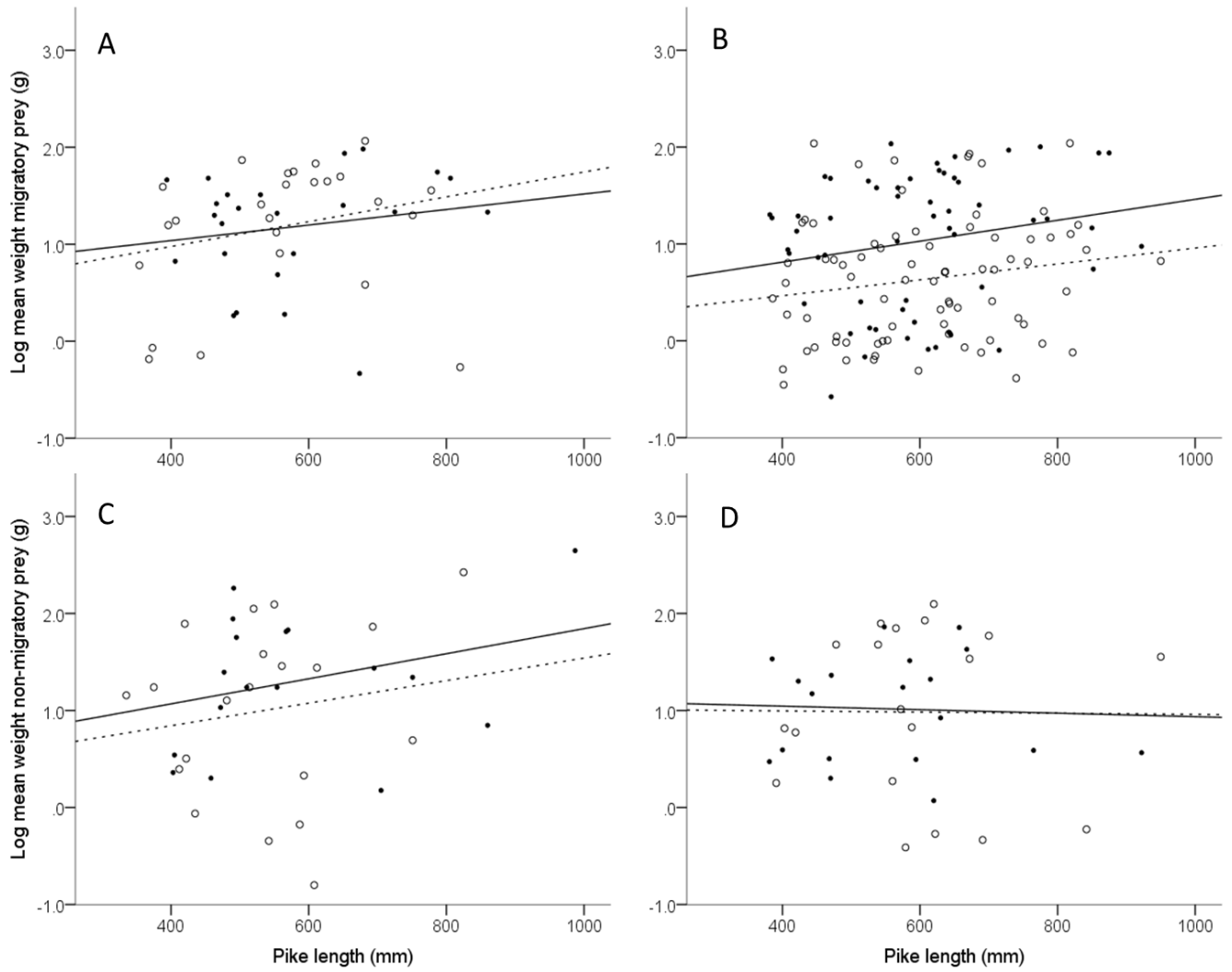


Figure S2: Estimated mean weight of migratory (A & B) and non-migratory prey fish (C & D) in pike stomachs in the residence (A & C) and migratory period (B & D) in open (open circles, broken line) and closed lakes (filled circles and full line) as a function of individual pike length.

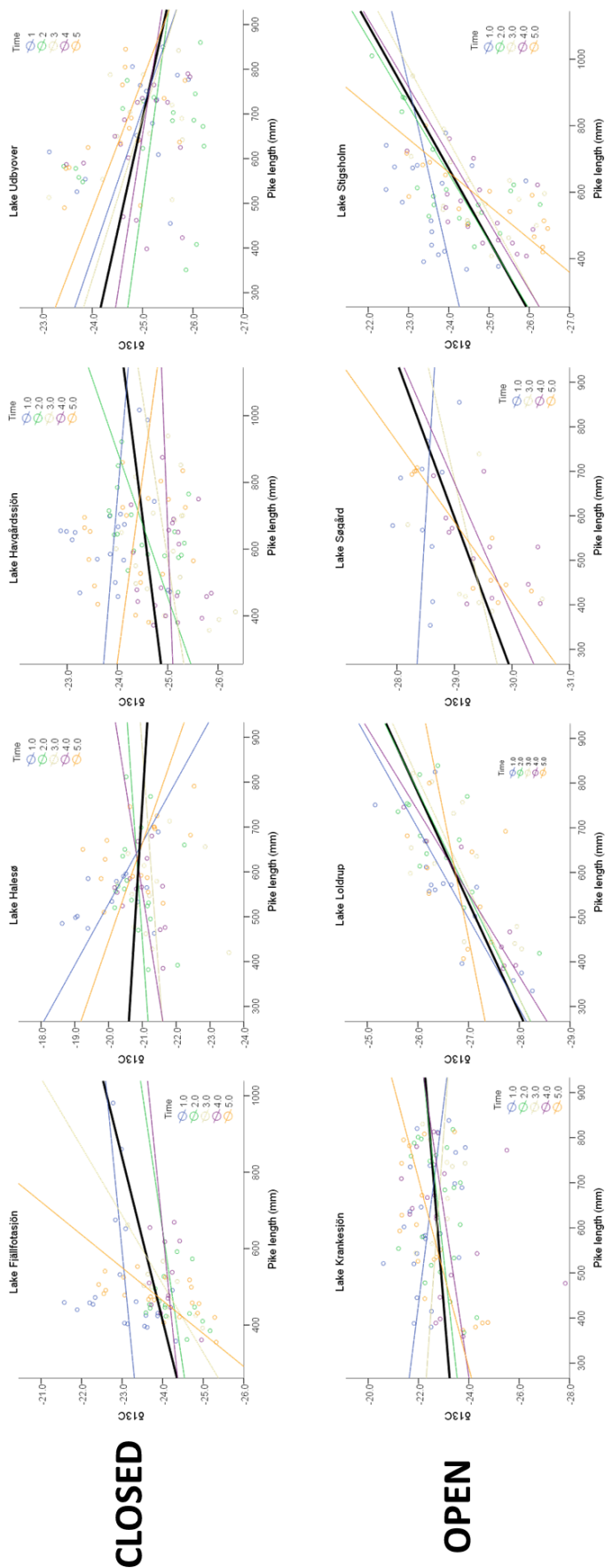


Figure S3: Lake specific regressions between stable carbon isotope values ($\delta^{13}\text{C}$) and pike length for different sampling events. Thick black lines indicate overall regression lines, whereas thin colored lines indicate regression lines for specific time periods. Note that slopes are generally more positive in open lakes and that blue lines (pre-migration sampling) generally have a less positive slope in the open lakes than regression lines for sampling events representing the migration period (purple, green, brown and orange lines).

PAPER II

Relationship between bream (*Abramis brama*) activity and water turbidity in a shallow lake under different season conditions



Relationship between bream (*Abramis brama*) activity and water turbidity in a shallow lake under different season conditions.

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Keywords: ecosystem engineers, benthivory, foraging activity, bioturbation, resuspension

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Abstract

Ecosystem engineers, such as benthivorous bream, disturb the lake sediment when foraging. Such disruption of sediment releases nutrients otherwise captured in the sediment back into the water column. Hence, foraging behaviour of benthivorous bream may aggravate water turbidity in shallow lakes. In order to investigate seasonal dynamics in bream activity and its impact on water turbidity under natural conditions, bream daily activity was studied from 2012 to 2016 in a shallow Danish lake using passive integrated transponder technology. During the same period water turbidity and temperature was measured. Results showed a clear relationship between bream activity and water turbidity, especially at water temperature below 15°C indicating that winter season activity of benthivorous bream may play an important role for maintaining lake ecosystems

in a turbid state. This is to our knowledge the first full-scale study under natural conditions to describe how bream activity influence lake turbidity on a day-to-day basis. Our findings adds a seasonal component to previous findings showing that benthivorous feeding bream are important ecosystem engineers with the potential to bring nutrients from the sediment into the water column leading to increased water turbidity and ultimately impact biodiversity and ecosystem functioning within shallow lakes.

Introduction

Many aquatic and terrestrial ecosystems exist in alternative states, whose stabilities are determined by their resistance to environmental change and their resilience (Peterson & Stevenson, 1992; Peterson et al., 1998; Gunderson, 2000; Folke et al., 2004). The mechanisms responsible for the degree of resilience are often understood through consumptive effects, although non-consumptive effects may be at least as important (Dublin et al., 1990). Non-consumptive effects that may affect ecosystem resilience include trampling, burrowing and horning in terrestrial ecosystems (Knapp et al., 1999; Estes et al., 2008; Haynes, 2012) and bioturbation, digging and burrowing in aquatic ecosystems (Moore, 2006). Large-bodied species of such ecosystem engineers (Jones et al., 1997) generally have a higher non-consumptive per capita effect on the ecosystem than smaller (Cumming & Cumming, 2003) and since large-bodied species generally have longer life spans, their population dynamics may not respond fast to ecological changes, which may increase their effect on ecosystem resilience. In shallow lakes, large bodied benthivorous fish are believed to maintain the ecosystem in a turbid state (Scheffer et al., 1993), but the actual mechanisms involved, especially regarding seasonal variation, are relatively poorly understood.

Eutrophication has historically had a severe effect on many aquatic ecosystems (Smith, 2003) including lakes (Brönmark & Hansson, 2002) and although many lakes now are in or have completed a phase of re-oligotrophication (Jeppesen, et al., 2005a), changes back towards the original state in several cases appear slow or absent (e.g. Ibelings et al., 2007). Eutrophication in lakes, caused by increased nutrient loadings from urban sewage and/or agricultural run offs, results in a cascading change of the lake ecosystem, including increased algal productivity and sometimes cyanobacteria bloom, increased density of planktivorous and benthivorous fish species, turbid water and a subsequent loss of submerged macrophytes and reduced biodiversity (Harper, 1992; Cooke et al., 1993; Carpenter et al., 1998; Jeppesen et al., 2005b). The increase in water turbidity associated with eutrophication is mainly caused by increased algal biomass. However, in shallow lakes,

turbidity can also be highly influenced by non-consumptive effects, i.e. by resuspension of sediment particles caused by foraging behaviour of benthivorous fish (Breukelaar et al., 1994; Zambrano et al., 2001; Parkos et al., 2003). Such resuspension of sediment can potentially influence the structure and functioning of the lake ecosystem in several ways (Scheffer, 1998). The immediate and direct effect is an increase in turbidity, caused by increased inorganic suspended material which reduces light penetration through the water column (Roberts et al., 1995; Parkos et al., 2003). This may influence foraging strategies of visual orientated piscivores, i.e. reduce foraging rates, and thereby potentially uncouple trophic top down cascades (Miner & Stein, 1993) and affect dispersal and growth of submerged macrophytes, due to less light available in the water column (Fisher et al., 2013; Gu et al., 2016).

Benthivorous fish can also negatively affect submerged macrophytes in other ways than by resuspension of sediments e.g. by uprooting due to the mechanic stress that benthivorous fish create on the sediment. Such uprooting may reduce submerged macrophyte densities or even prevent establishment of any new macrophytes (King & Hunt, 1967; Roberts et al., 1995; Parkos et al., 2003). In addition, excretion from high density populations of benthivorous fish can provide nutrients for increased epiphytic growth on submerged macrophytes that can also cause a reduction in distribution of submerged macrophytes (Williams et al., 2002). The disappearance of submerged macrophytes can have strong effects on the lake ecosystem as they play an important structuring role, especially in shallow lakes (Scheffer et al., 1993; Jeppesen et al., 1997).

Another non-consumptive ecosystem effect of large bodied benthivorous fish is an increase in total phosphorus and nitrogen concentrations due to resuspension, releasing sedimentary nutrients to the water column, which ultimately can result in increased growth of algal biomass (Boström et al., 1982; Andersson et al., 1988; Parkos et al., 2003; Fisher et al., 2013; Gu et al., 2016). Hence, benthivorous fish can have profound effects on other trophic levels and play an important role for maintaining lakes in, or shifting lakes towards a turbid stable state, which may have severe negative impacts on biodiversity as well as ecosystem functioning (Scheffer, 1990).

In northern European lakes, bream (*Abramis brama*) is a common and abundant freshwater fish (Tammi et al., 1999; Kottelat & Freyhof, 2007). Individuals generally display ontogenetic diet shifts, with young bream feeding mainly on planktonic prey and adults mainly feeding on benthivorous prey (e.g. Persson & Hansson, 1999, but see Lammens et al., 1987 for exceptions). Adults are specialized benthivorous, foraging by penetrating and probing the sediment, ingesting both food organisms (detritus, insect larvae and worms) and sediment particles (Breukelaar et al.,

1994; Persson & Hansson, 1999). Within the buccal cavity, food particles are selectively retained, whereas sediment particles pass the gill raker system and are flushed away in clouds behind the opercula into the water column (Lammens & Hoogenboezem, 1991). The feeding behaviour of large adult bream can therefore cause profound resuspension of lake sediments, as illustrated by Winkel & Davids (1985) who estimated that from October to May about 100% of the bottom surface in the shallow parts of a Dutch lake was disturbed by foraging bream. Thereby they reduce water visibility, decrease sediment stability and release nutrients from the sediment into the water column (Andersson et al., 1988; Meijer et al., 1990; Brukelaar et al., 1994). Due to their large adult size, older bream are generally outside the predatory range of piscivorous fish (e.g. Skov et al., 2011), which in combination with a high longevity (Kottelat & Freyhof, 2007) results in a slow population response to changed environmental conditions. Consequently, bream is a target species in biomanipulation by fish removal, i.e. as a tool for restoration of eutrophic shallow lakes which often include high densities of large adult bream (Jagtman et al., 1990; Søndergaard et al., 2008). Despite the important role that bream have for ecosystem functioning in shallow lakes and as target species in biomanipulation, studies exploring the direct relationship between bream activity and turbidity are lacking. Instead, most studies that have explored presence vs. absence of bream and the related changes in turbidity either in enclosures (e.g. Breukelaar et al., 1994) or under natural conditions (e.g. Meijer et al., 1990). Further, most studies on benthivorous fish have in general focused on summer dynamics and not included any seasonal dynamics in their studies (but see King & Hunt, 1967). As for ectotherms in general, bream activity, such as foraging intensity, is expected to be positively related to temperature. However, telemetry studies have shown considerable activity of lentic freshwater fish, such as bream, also during cold periods in autumn and winter (e.g. Jacobsen et al., 2002; Baktoft et al., 2012). This could in turn have implications for seasonal dynamics of water turbidity. The aim of this study is therefore to increase our knowledge about the seasonal dynamics in bream activity and how this impact water turbidity in shallow lakes under natural conditions. To obtain this, we measured bream activity daily for four years using biotelemetry technology, and related this to daily on-site registrations of water turbidity during the same period.

Methods

Study system and study period

The study was conducted in Lake Loldrup, which is 0.39 km², shallow (mean depth 1.2 m, maximum depth 3.3 m), slightly eutrophic (mean Secchi depth 1.1 m) and situated in Denmark (56°29'N, 9°26'E). The lake has an inlet and outlet stream (Fig. 1). The fish community is dominated by roach (*Rutilus rutilus*) and bream (*Abramis brama*), but also includes perch (*Perca fluviatilis*), pike (*Esox lucius*), white bream (*Blicca bjoerkna*) and pikeperch (*Sander lucioperca*). The study was initiated in June 2012 and terminated in August 2016.

Bream activity

To track activity of bream we used passive biotelemetry technology, i.e. a modified Passive Integrated Transponder (PIT)-tag antenna system (e.g. Skov et al., 2008). Three pair of antennas was positioned in the lake in 2012 (Fig. 1). Each antenna is loop shaped and constructed by oxygen free copper loudspeaker cable (2 · 4 mm²) mounted inside a frame (dimensions 500 cm · 85 cm) of 30 mm PVC pipe, which are mounted perpendicular to the lake bed by wooden posts. Each pair of antennas was composed of one antenna in the interface between vegetation and open water and one antenna on average 30 meter further ashore in the limnetic zone (Fig. 1). The three sets of hardware each connected to a pair of antennas, were powered directly from the power net (two pairs of antennas) or from a small wind mill (Rutland, Model 913; 12 volt 85 watt).

As part of this and other studies (e.g., Skov et al., 2011), pit tagging of bream had been conducted in Lake Loldrup every fall from 2006 to 2016. Bream for tagging were caught in fall by electrofishing, seining and gill netting (emptied at least every second hour). Hereafter, they were anaesthetized with benzocaine (20 mg L⁻¹), individually measured for total length (nearest mm) and body mass (nearest g) before tagged by surgically implanting a passive integrated transponder (PIT)

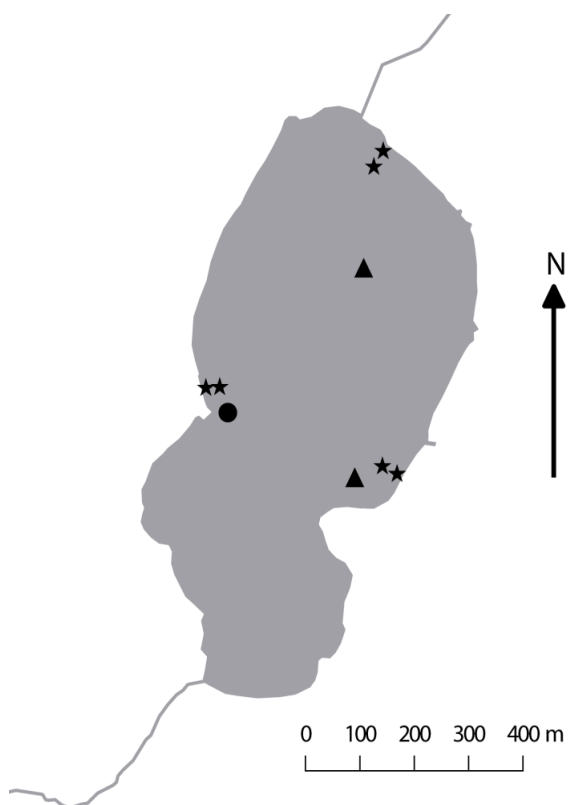


Figure 1: Lake Loldrup including the position of the six antennae (stars), turbidity logger (circle), and the sites of Secchi depth measurements (triangles).

tag (Texas Instruments, RI-TRP-RRHP, Plano, Texas, USA, half duplex, 134 kHz, 23.1 mm long, 3.85 mm in diameter, 0.6 g in air) into the body cavity of the fish. Following PIT tagging, fish were allowed to recover until released to the lake again. A total of 726 adult bream (434.5 ± 62.2 mm, mean total length \pm SD) was tagged between 2006 and 2016.

When a tagged bream swims by any of the six antennas placed in the lake (Fig. 1), the PIT-tag is energized and its unique code emitted. This is recorded by special software and transmitted once a day via GPRS Net to a database at DTU Aqua where it is stored together with date, time and the identity of the antenna. As a measure of bream activity levels we constructed an activity index (hereafter bream activity), based on the number of unique individual bream registered per antennae per hour. The mean number of bream per antenna was then calculated per day resulting in a daily estimate, i.e. bream activity.

Efficiency of the antenna, i.e. the amount of time when the antennas was functioning was also evaluated, and only periods where two or more of the six antennas were functioning was included in the analyses. This evaluation was based on so-called “marker tags”, placed in the near vicinity of each antenna. This special tag emits a code every hour and we subsequently identified days of malfunctioning as days where no code from the marker tag was registered and, at the same time, no tagged fish were registered. The latter to prevent exclusion of days where it was the marker tag, and not the antenna, that was malfunctioning. The six antennas were functioning 90% of the time during the study period. Most often it was a single or a pair of antennas that was malfunctioning for a period (rarely more than a few weeks), and more rarely 3 and 4 antennas ($< 4\%$ of the days) was malfunctioning. The reasons for malfunctions were most often battery failures and typically related to the wind powered pairs of antenna where calm weather prevented the batteries to charge. Experimental animal treatment was performed under permission from the Danish Animal Experiments Inspectorate.

Water temperature and turbidity

Turbidity, the amount of light that is scattered by material in the water, as well as water temperature was measured throughout the study period using AQUAlogger® 210TYT, Aquatec, Basinstroke, UK (300 mm long · 60 mm, diameter). The turbidimeter was attached to a fixed structure (wooden pole) approximately 0.5 meters below the water surface and measured water turbidity in Formazin Turbidity Units (FTU) and temperature (Fig. 1). Turbidity was measured using optical backscatter, which detect optical scattering of infrared light from suspended matter. The AQUAlogger®

210TYT uses an 850 nm light source and, within the range of 0-750 FTU it measures turbidity linearly with a deviation of < 2%. To avoid biological growth on the optical window of the logger, it was equipped with an antifouling wiper. Turbidity was measured five times minimum every second hour during the four-year study period from which the daily mean was calculated. The turbidimeter had about 40 days with malfunctioning, i.e. 3.38% of the study period and these days were excluded from the study.

As a way to translate FTU to Secchi depths, we measured Secchi depths at regular intervals from 2013 to 2016. Secchi depths were measured at one of two positions in the lake. However, on two occurrences Secchi depth were measured at both positions at the same day. On these days a mean of the Secchi depth was used in the relationship between turbidity (FTU) and Secchi depth (Fig. 1; Supplementary table 2).

Statistical analyses

To evaluate the role of bream activity on water turbidity in Lake Loldrup we applied Gamma distributed generalized additive models (GAM). The residuals were checked for absence of autocorrelation and variance homogeneity to meet the assumptions of the model. Prior to fitting the GAMs, Variance Inflation Factors (VIFs) were used to explore collinearity between covariates and only covariates with VIFs below 3 were used in the model (Zuur et al., 2009). This best model was chosen based on a stepwise selection method that optimized explained deviance and Akaike's Information Criterion (AIC). To account for environmental factors that might affect turbidity, we included daily averages of wind speed (m s^{-1}) and wind direction measured by the Danish Meteorological Institute in the vicinity of Lake Loldrup (9 km away; latitude: 56.49, longitude: 9.57).

The following GAM was fitted:

$\text{Turbidity} = \alpha + f_i(\text{Bream activity:Temperature}) + f(\text{Wind speed}) + f(\text{Wind direction}) + \text{Antenna} + \text{Year}$,
where α is the overall intercept, $f_i(\text{Bream activity:Temperature})$ is a smoothing function modelling a tensor product interaction between bream activity and water temperature, $f(\text{Wind speed})$ is a smoothing spline of wind speed, $f(\text{Wind direction})$ is a cyclic cubic regression spline. Antenna is the six antennas situated in the lake and is included in the model to account for antenna specific variation in bream activity and differences in functionality throughout the four years of analysis. Finally, Year is included as a factor to allow between year variation from 2012 to 2016. In order to

ensure that only benthivorous feeding bream were included, we exclusively included bream of minimum 30 cm in the model (Lammens et al., 1987; Persson & Hansson 1999). Preliminary data visualization revealed that bream activity was extraordinarily high in short periods during spring/summer each year, which most probably represent spawning behaviour rather than feeding activity. In accordance with Poncin et al. (1996) we define spawning period during spring/early summer as days with water temperature above 14.5°C and we set the start and finish of the spawning periods as days where bream activity sudden increased and decreased with minimum 50% according to the day before or after, respectively (Supplementary table 1, Fig. 2). Since the overarching goal of the study was to explore the general relationship between bream feeding activity and water turbidity, we excluded these data from the analyses.

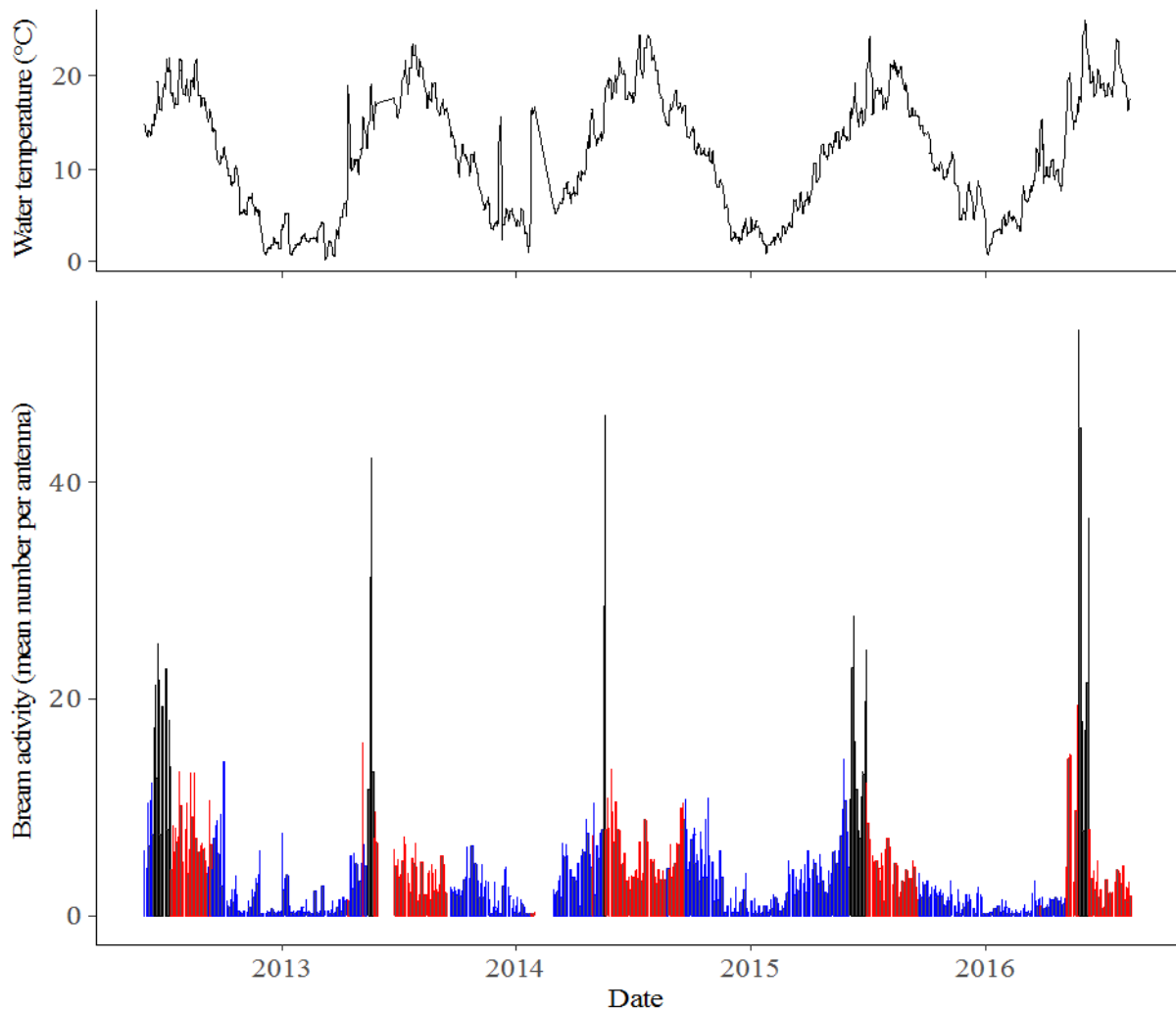


Figure 2: Daily water temperature (line) and bream activity (mean number of unique individual bream per antenna) during the study period. Blue bars for bream activity shows activity when water temperature is below 15°C and red bars with water temperature above 15°C. No bars illustrate days where data is lacking and black bars indicate days that we define as spawning activity which is not included in the GAM model. See text and supplementary table 1 for further explanations.

Table 1: Statistical results from the generalized additive model (GAM), $Turbidity = \alpha + f_t(\text{Bream activity:Temperature}) + f(\text{Wind speed}) + f(\text{Wind direction}) + \text{Antenna} + \text{Year}$. Deviance explained by this model is 75.1% and $R^2 = 0.63$.

Categorical variables	F-value	p-value
Antenna	5.09	<0.001
Year	82.54	<0.001
Smoothing functions	F-value	p-value
Bream activity:Temperature	6.91	<0.001
Bream activity	3.37	0.003
Temperature	2268.76	<0.001
Wind speed	26.84	<0.001
Wind direction	3.74	<0.001

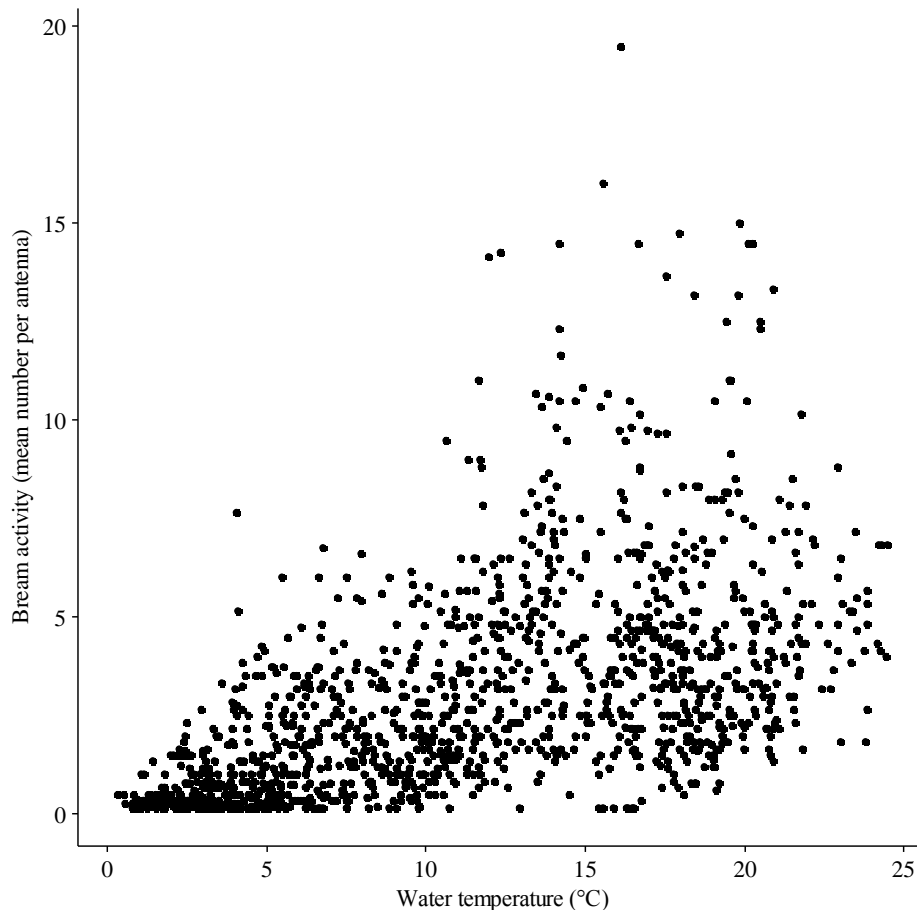
We preliminary tested if a delay between time of bream activity and water turbidity would produce a better AIC. However, this was not the case and we included bream activity and water turbidity measured on the same day in the model (Supplementary table 3).

In addition to the GAM analysis, temperature dependent bream activity patterns were explored by a correlation between bream activity and the average daily water temperature. Further, a simple correlation was used to illustrate the relationship between FTU turbidity and Secchi depths (Supplementary table 2).

All statistical analyses were carried out using the statistical computing program R (R Core Team, 2016) and the GAM model was performed using the *mgcv* package (Wood, 2011).

Results

From June 2012 to August 2016, a total of 448 different pit-tagged bream > 300 mm in total length were recorded on the six antennas in Lake Loldrup. Registrations occurred throughout the study period but there was a clear relationship between bream activity and temperature ($R^2 = 0.46$), illustrating higher activity during the summer period (Fig. 2 & 3).



*Figure 3:
Relationship between
water temperature
(°C) and bream
activity (mean
number of unique
individual bream per
antenna) ($R^2 = 0.46$).
Bream spawning
activity is not
included in this figure
(see text for further
explanation).*

As expected there was a clear relationship between FTU and Secchi depth ($R^2=0.70$) (Fig. 4), confirming that our one point high-resolution monitoring of turbidity well represent the two Secchi depth points in the lake.

Bream activity affected turbidity, although this effect was influenced by temperature (GAM, $p < 0.001$, Table 1, Fig. 5). Indeed, there is an increase in turbidity with increasing temperature, but bream activity appears to result in increased water turbidity when the temperature is relatively low i.e. below approximately 15°C (Fig. 5) and at Secchi depths between 60 and 200 cm (Fig. 4). At higher water temperatures, where Secchi depths were always < 60 cm (Fig. 4), the relationship between bream activity and turbidity was not as obvious (Fig. 5). Additionally, wind speed and

wind direction (Fig. 6) were significant predictors of water turbidity in the model ($p < 0.001$, Table 1). Wind speed increased turbidity and wind direction influenced turbidity particular at East and West directions (Fig. 6). Also year and antenna were significant predictors of water turbidity ($p < 0.001$, Table 1), which presumably is just an expression of variation between year and antenna (not all antenna were working probably all the time).

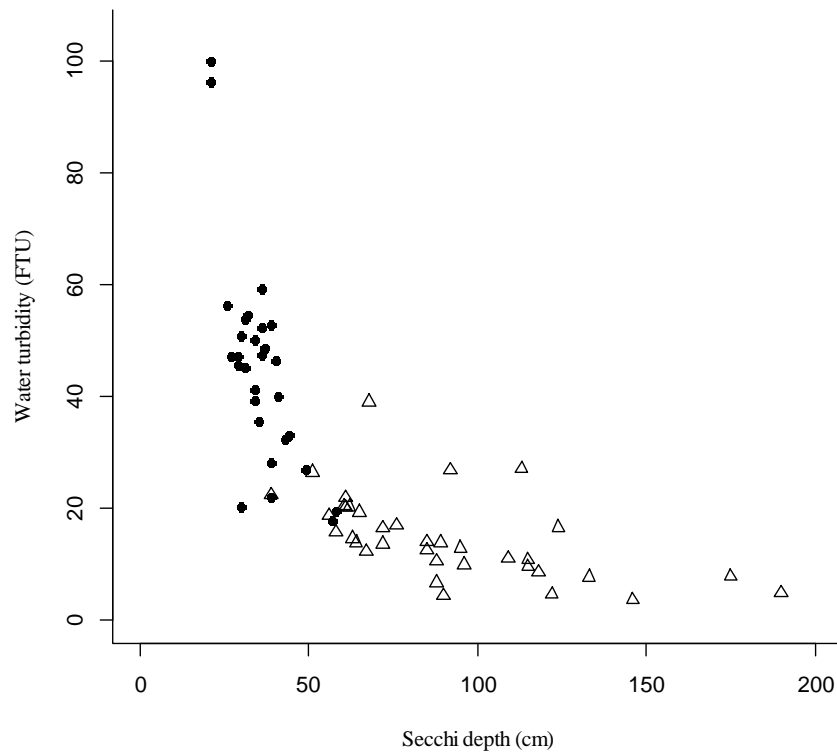


Figure 4: Relationship between turbidity (FTU) and Secchi depth (cm) ($R^2 = 0.70$) measured in Lake Loldrup from 2013 to 2016 on dates were temperature was above 15°C (filled circles) and below 15°C (triangles). See supplementary table 2 for sampling dates.

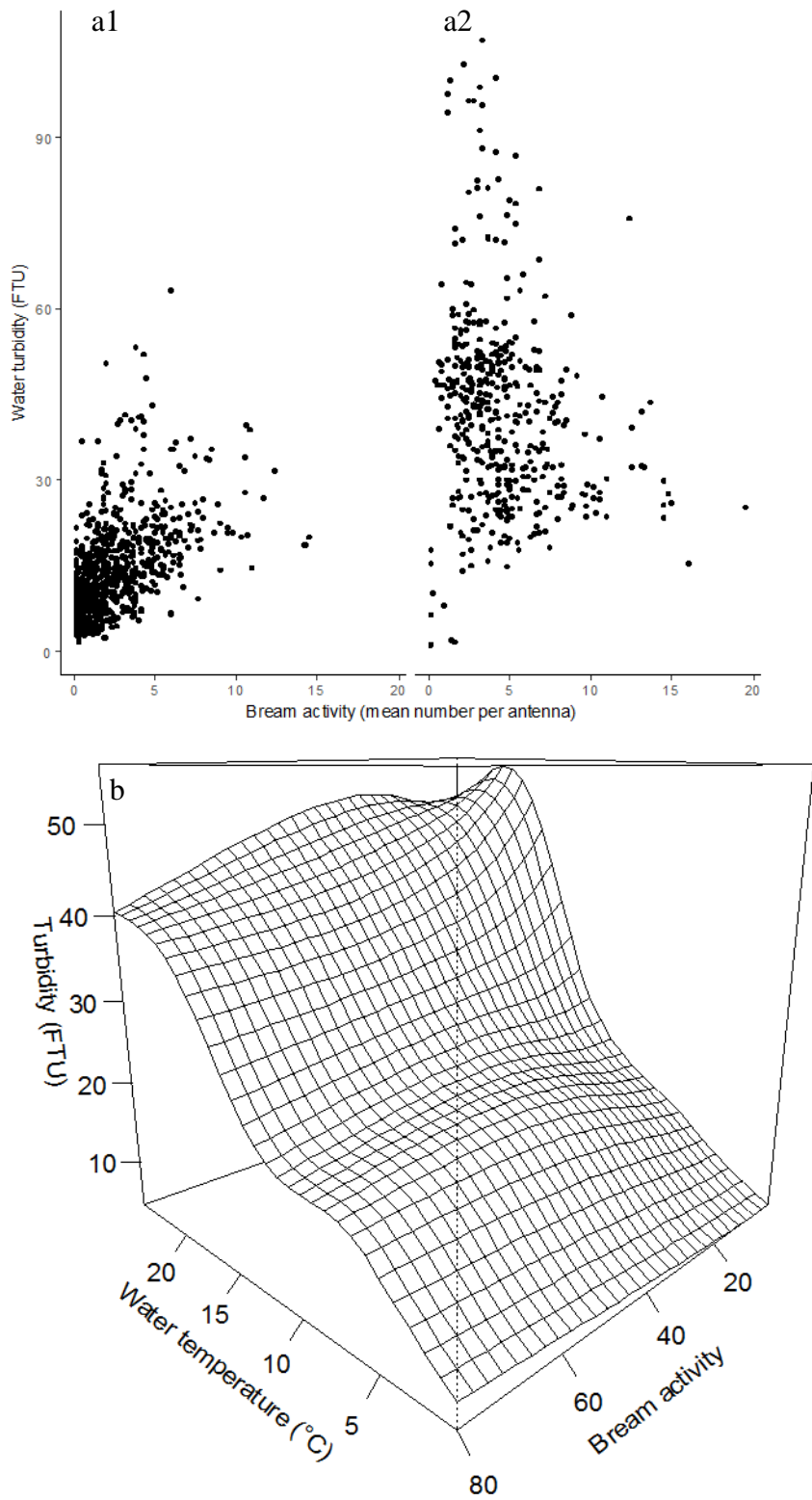


Figure 5: The relationship between bream activity and water turbidity (FTU) shown as raw data separated between days where average temperature was below (a1) and above 15°C (a2) and 3D plot showing the model output of how the interaction of water temperature and bream activity (n) predicts turbidity (b).

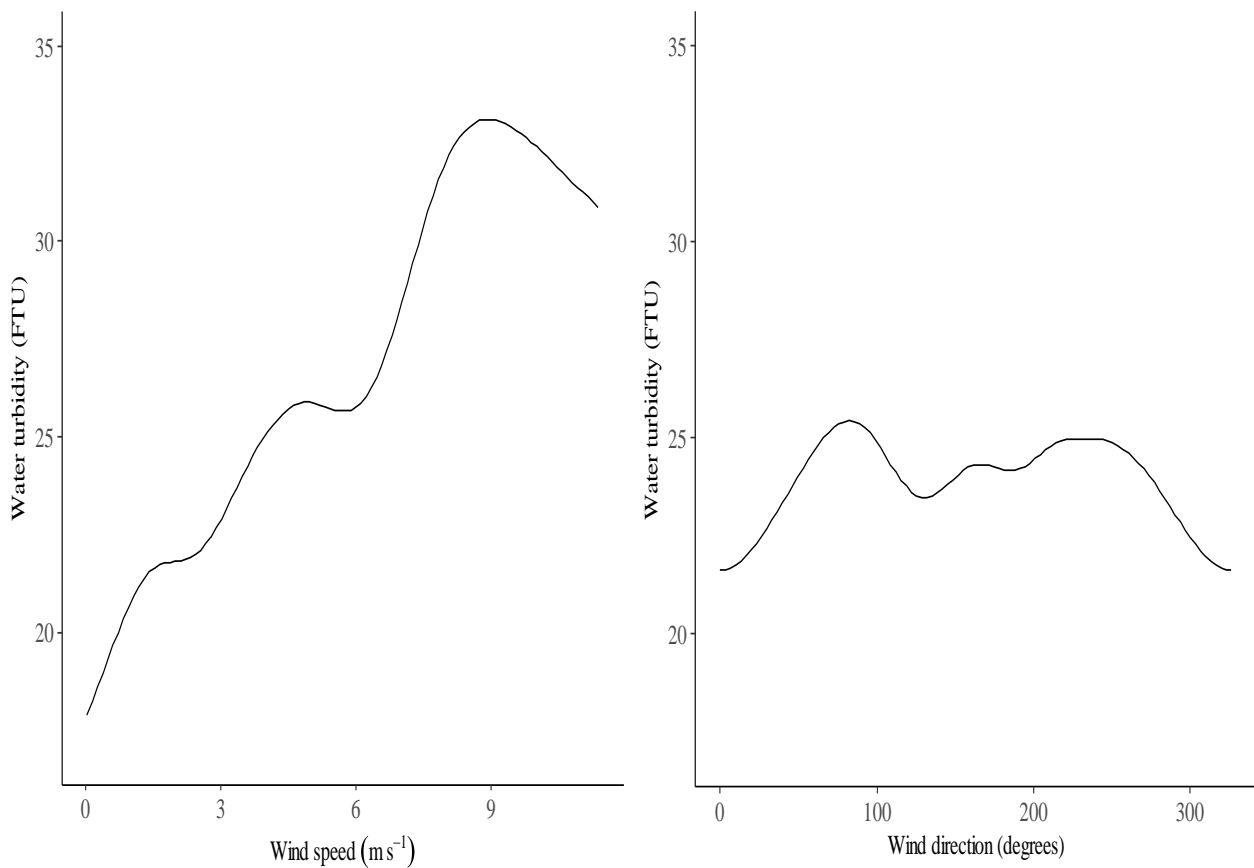


Figure 6: Model plot of the relationship between wind speed ($m s^{-1}$), wind direction (degrees) and water turbidity with temperature and bream activity held constant.

Discussion

This study highlights the specific influence of variation in activity of large-bodied ecosystem engineers on ecosystem state variables that are central for ecosystem resilience through non-consumptive mechanisms. More specifically, we demonstrate how temperature dependent activity patterns of large-bodied bream influence sediment resuspension, i.e. water turbidity, on a daily basis. Peaks in bream activity occurred, as expected, mainly during summer but bream activity at least to a certain extent, persisted even at low temperatures. This is in line with other studies that have shown that lentic fish can be relative active during the winter season (Jacobsen et al., 2002; Baktoft et al., 2012). The present study aligns with previous studies, suggesting a relationship between presence of bream and water turbidity (Andersson et al., 1978; Breukelaar et al., 1994; Winkel & Davids, 1985; Meijer et al., 1990). However, most of these have been conducted under experimental conditions, i.e. small enclosures, and none of these studies have included seasonal variation. Further, these studies have not strictly focused on the daily relationship between bream activity and resulting changes in turbidity, but instead on more general relationships between

averages of bream biomass and corresponding water turbidity. Accordingly, this is to our knowledge the first full-scale study under natural conditions to describe seasonal patterns in bream activity and directly demonstrate how increased bream activity influence lake turbidity on a day to day basis.

From a lake ecosystem perspective, it is interesting that our results predict that bream activity influence turbidity only when water temperature is relatively low, i.e. below 15°C. For example at temperatures below 15°C, no turbidity below 15-20 FTU, reflecting Secchi depths of above 60cm (Fig. 5), was registered when the bream activity index was > 30 pr. day) (Fig. 5a). These patterns, hence, suggests that bream activity in the cold period likely caused considerable variations in light penetration through the water column in Lake Loldrup during the four year study period.

Previous studies have shown that benthivorous fish including bream (Breukelaar et al., 1994; Zambrano et al., 2001; Parkos et al., 2003) can have negative effects on abundance of submerged macrophytes due to impaired light conditions due to resuspended material and through uprooting of plants. The general high activity of bream during the cold period and the resulting effect on water turbidity, suggests that such effects can occur even during the winter season. We tentatively suggest that the negative effects in fact could be most profound during spring when the submerged macrophytes are small and depend on optimal light conditions near the sediment surface. In addition to shading of light through the water column, the establishment of macrophytes could also be impaired by spring bream activity. During spring, young macrophytes are more fragile and therefore under higher risk to be uprooted. This assumption is supported by King & Hunt, (1967) who argued that benthivorous carp in enclosures had strong impact on submerged vegetation in May when the vegetation was still young. It is well established that submerged macrophytes plays an important role in stabilizing shallow lakes in a clear-water state (Scheffer et al., 1993; Jeppesen et al., 1997) i.e. they bind nutrients and reduce sediment resuspension by wind (Donk & Bund, 2002; Nurminen & Horppila, 2009). Hence, winter season activity of bream may therefore play a role for maintaining lakes in a turbid state, by preventing spring establishment of submerged macrophytes. Ultimately, this can lead to reduced biodiversity as submerged macrophytes promote species diversity by providing habitat and food for a range of organisms (Declerck et al., 2007).

Benthivorous fish may provide an important link between the pelagic and benthic systems of the lake ecosystem, e.g. by bringing nutrients from the benthic to the pelagic zone (Lamarra, 1975; Andersson et al., 1988; Vanni, 2002; Huser et al., 2016). This study suggests that such mechanisms may be important not only in summer, but throughout the whole year. Kristensen et al. (1992) showed how wind induced resuspension resulted in increased phosphorous concentrations in the lake water during winter season. Hence, it is likely that resuspension by benthivores could have similar impact on winter season concentrations of nutrients and future studies should detangle how this increased nutrient loading could influence primary production in shallow lakes.

This study found no relationship between bream activity and turbidity at temperatures above 15°C. This does not mean that such relationship is non-existing at higher temperatures as several studies have measured impacts of bream biomass on water turbidity at temperatures above 15°C (e.g., Breukelaar et al., 1994; Meijer et al., 1990). Instead, we suggest that phytoplankton productivity in Lake Loldrup became the main driver of turbidity during summer, potentially obscuring any additive effects of increased sediment suspension caused by bream. In relation to this, we recommend that any future study of this kind include a fractionation of the measured turbidity, i.e. separation into phytoplankton and inorganic suspended solids, respectively. Clearly, this will be a useful supplement to the FTU vs. Secchi depth calibration that the present study is built on, and give more knowledge on the role of bream activity on turbidity during summer.

Our study and statistical analyses were designed to elucidate the role of bream activity and temperature on water turbidity with inclusion of wind conditions as factors. Especially wind conditions have in many studies been shown to affect turbidity through resuspension of sediment especially in large shallow lakes (e.g. Kristensen et al., 1992; Eleveld, 2012; Chung et al., 2009; Meijer et al., 1990; Huser et al., 2016). However, since Lake Loldrup is a small lake with the longest fetch of only 800 m and since this is north-south orientated and the prevailing wind direction is west-east, we did not anticipate wind to play any major role for turbidity in this study. However, there appeared to be a clear relationship between wind speed and water turbidity suggesting that even in small shallow lakes wind induced resuspension can play an important role. Moreover, the strongest effect was seen when the wind was in the prevailing west/east direction. This is surprising, because the west/east fetch is only around 350 meter and because previous studies have shown that the highest resuspension potential is normally located on the lee side of the prevailing wind directions, i.e. the prevailing winds erode the bottom on one side of the lake,

depositing resuspended material predominantly on the opposite side, where it can be resuspended by winds from non-prevailing directions (Löfstedt & Bengtson, 2008).

Since wind appeared to play a larger role than expected, we investigated potential interaction between bream activity and wind speed in the winter season, using the GAM model but only with water temperatures $< 15^{\circ}\text{C}$, as we expected wind to blur any effects of bream activity at high wind speeds. This examination revealed, rather surprisingly, that bream activity influenced turbidity independently of wind speed, i.e. that the resuspension effects from bream is unaffected of wind speeds, at least up to wind speeds of 10 m s^{-1} (Fig. 7). In relation to the overall influence of wind, the resuspension activities of benthivorous fish may play an enhancing role as they prevent sediment consolidation, which likely increase resuspension in windy periods.

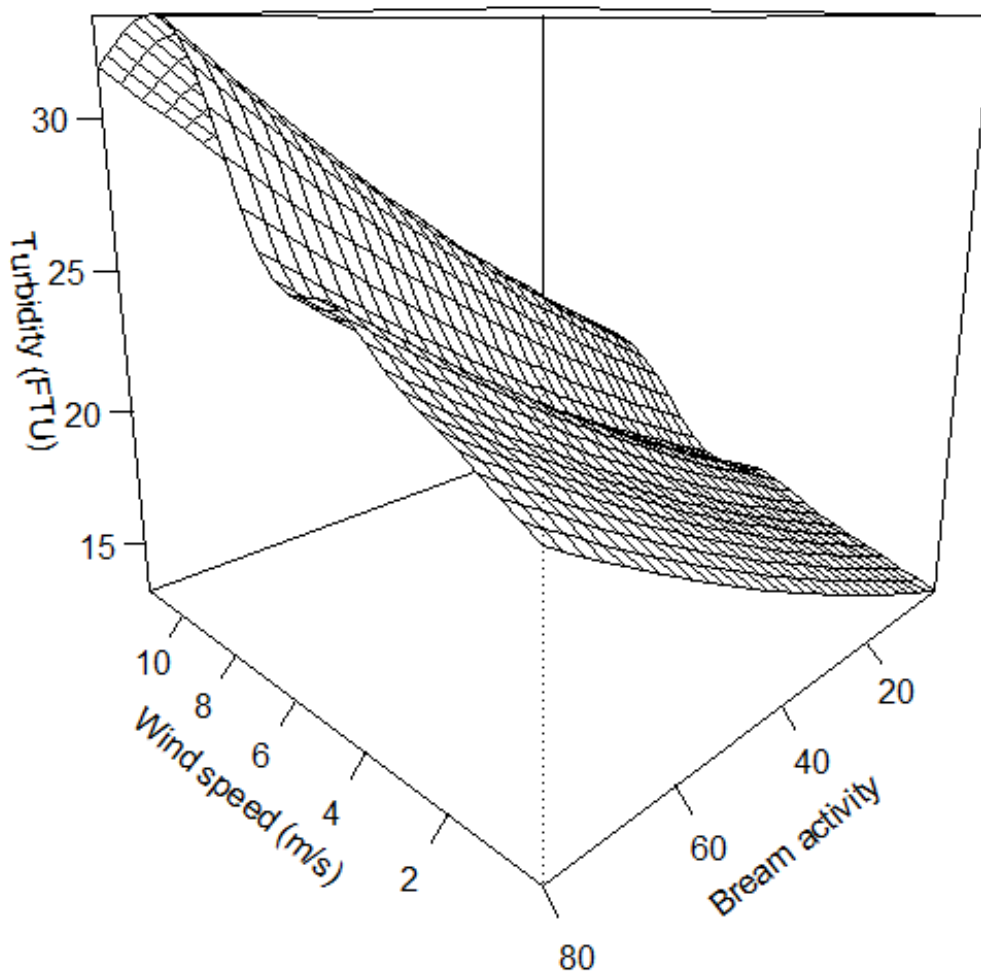


Figure 7: 3D plot of GAM model illustrating the relationship between wind speed (m s^{-1}) and bream activity (n) at water temperatures below 15°C . Testing the interaction between bream activity and wind speed shows a non-significant ($p > 0.05$) relationship.

We excluded periods with presumed spawning activity from our data set, as we aimed to explore the relationship between bream activity and turbidity exclusively during periods where feeding was the dominant cause of activity. The exclusion of data was based on the knowledge that bream spawn in spring at temperatures above 14.5°C (Poncin et al., 1996). Accordingly, we excluded spawning periods between mid-May to mid-July of varying lengths probably reflecting variation in spawning synchronicity between years (see Fig. 2 and supplementary table 1). The clear relationship between bream activity and turbidity that we found at temperatures below 15°C supports that we successfully managed to exclude the periods of spawning activity and that the majority of activity data in the dataset was indeed related to foraging.

One could argue that the relationship between bream activity and turbidity is causal in the opposite direction, i.e. it reflects that bream prefer to be active in turbid water, e.g. as a way to reduce predation risk from visual predators. However, bream > 300 mm have outgrown the gape size of most predators (Skov et al., 2011) and therefore we argue that movements due to predation avoidance probably play a minor role, although we acknowledge that a “ghost of predation past” (Mehner & Hölker, 2004) could have had an influence. Also, if bream activity was dictated by water visibility we would have expected to see a clear relationship between FTU and activity also at temperature > 15°C, where piscivorous fish generally are particularly active, but this was not the case. Furthermore, at temperatures < 15°C, where wind speed plays a clear role for FTU this argument would also predict that bream activity always should be high at high wind speeds, but this appeared not to be the case (Fig. 7).

Previous studies have demonstrated a link between biomass of bream and turbidity (Breukelaar et al., 1994; Meijer et al., 1990). In the present study, we had no information about biomass and could not make this link. However, the population density of tagged bream in Lake Loldrup was most likely not constant throughout the study period as mortality of old individuals probably occurred as did immigrations/emigrations to and from the lake (J. H. Hansen, personal observations) and furthermore new bream were tagged every year. Still this potential variation in density of tagged bream, which also is partially accounted for in the year effect in the model, was not strong enough to mask the relationship between bream activity and water turbidity, at least at temperatures below 15°C, which we therefore argue is robust. We assume that turbidity measured with our turbidimeter fixed at a single position in the lake throughout the lake was representative for overall turbidity in

the lake. Clearly, it would have been ideal to have had several spatial separated turbidity measurements, but the clear relationship between FTU and Secchi depth, which was measured at two different points in the lake, supports that our single point observation is representative. The lack of information on the stability of bream density clearly impairs discussion of how variation in bream biomass (if any) influenced the fluctuations in turbidity and if any threshold biomass levels should exist where bream biomass would be too low to have impact on turbidity.

In conclusion, this study illustrates how non-consumptive effects of large bodied ecosystem engineers can affect aquatic ecosystems and potentially influence the stable state in shallow lakes. More specific we have shown, on a daily basis, how activity of large bodied benthivorous bream influence water turbidity in a small shallow lake, especially at temperatures below 15°C. This implies that winter season activity of bream may play a role for maintaining lake ecosystems in a turbid state, e.g. by bringing nutrients from the benthic into the pelagic and by preventing spring establishment of submerged macrophytes through shading or mechanical stress. Ultimately this can lead to reduced biodiversity as submerged macrophytes promote species diversity by providing habitat and food for a range of organisms.

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Supplementary material

Supplementary table 1: Dates identified as spawning days and removed from the GAM model. Spawning days are defined as days during the spring or early summer with water temperature above 14.5°C and bounded by sudden increases/decreases in activity of minimum 50% from one day to another.

Year	Date (month-day)
2012	June-15 – July-11
2013	May-16 – May-22
2014	May-18 – May-20
2015	June-5 – June-30
2016	May-26 – June-11

Supplementary table 2: Sampling dates of Secchi depth in Lake Loldrup. † indicate Secchi depth measured twice that day and the mean of these measurements are included in the analysis.

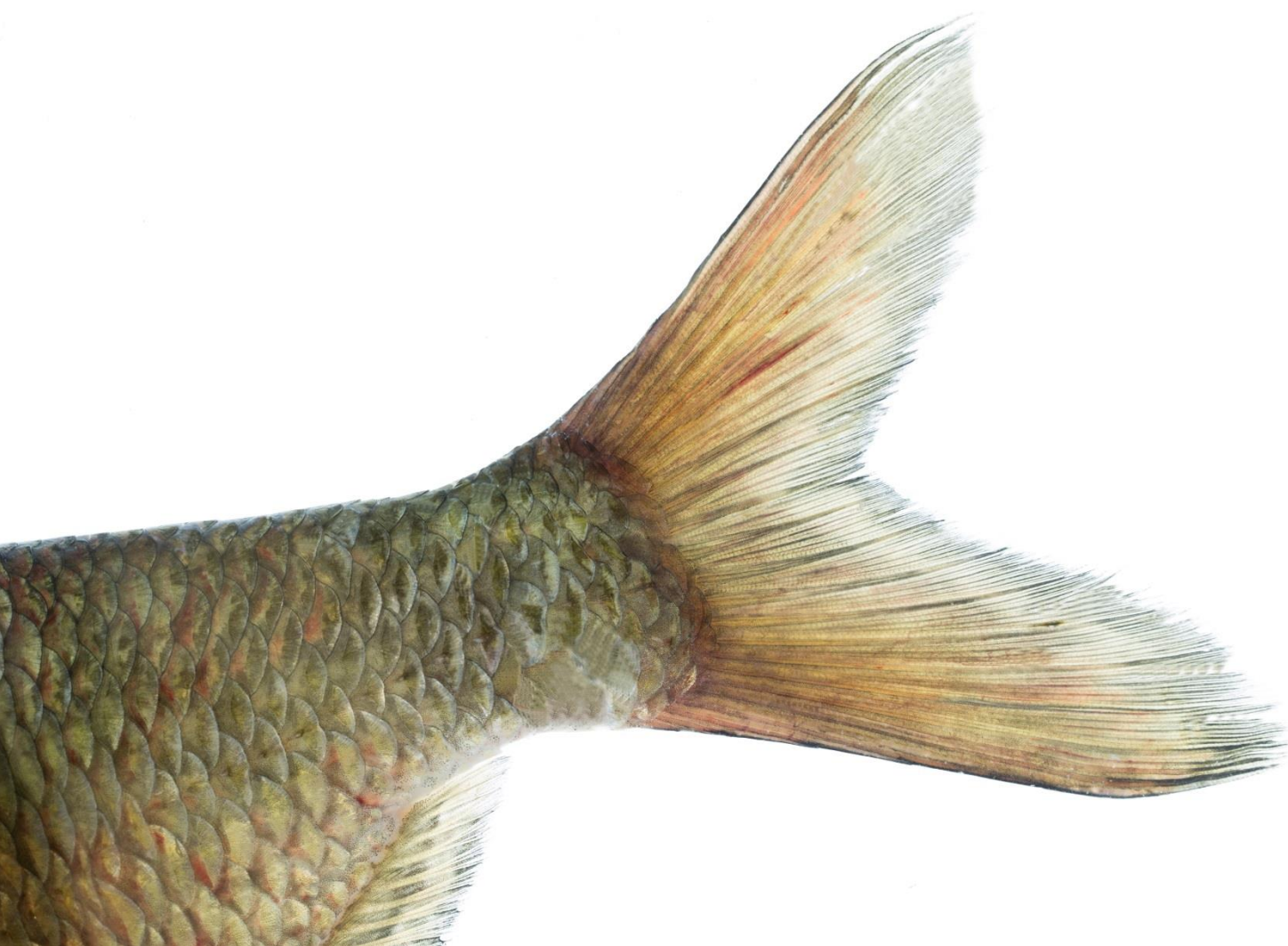
Year	Month	Day
2013	May	8
2013	August	7
2013	September	6 + 28
2013	October	5 + 23
2013	November	12
2013	December	10
2014	January	15
2014	February	17
2014	March	6
2014	April	11
2014	May	8
2014	June	2 + 10 + 17 + 20
2014	July	3 + 9 + 18
2014	August	12 + 20 + 23
2014	September	19
2014	October	8 + 16 + 23 + 31
2014	November	6
2014	December	3 + 5
2015	January	5 + 13 + 14 + 22
2015	February	16 + 18 + 25
2015	Mach	12 + 18 + 27
2015	April	13 + 14
2015	May	5 + 12 [†] + 29
2015	June	10 [†] + 23
2015	July	3 + 15
2015	August	13 + 17
2015	September	10 + 18
2015	October	8 + 12 + 27
2015	November	10 + 23
2015	December	1
2016	June	3 + 20
2016	July	6 + 13
2016	August	19
2016	September	15 + 22

Supplementary table 3: Akaike's Information Criterion (AIC) values for the different GAM models regarding delayed turbidity in relation to bream activity. The model with the lowest AIC-value is where turbidity is not delayed (Turbidity delayed 0 days) and therefore used in this study.

Model	AIC-value
Turbidity delayed 0 days	33500.7
Turbidity delayed 1 day	34189.7
Turbidity delayed 2 days	34322.8
Turbidity delayed 3 days	34544.3
Turbidity delayed 4 days	34881.4

PAPER III

Partial nomadism in large-bodied bream (*Abramis brama*)



Partial nomadism in large-bodied bream (*Abramis brama*)

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Keywords: Benthivore, dispersal, freshwater systems, resuspension, behavior

Abstract

Movement results in a diverse array of spatial- and temporal changes in the density of populations. The recent focus on a common movement ecology paradigm has increased awareness about the importance of distinguishing different movement patterns for understanding their specific impact on animal ecology and evolution. One specific form of movement is nomadism, where animals move between habitats in an arrhythmic fashion. Although not yet described for fish, nomadism within drainage systems would have large potential to disrupt local lake food webs in an unpredictable fashion. In this study, we used passive telemetry technology to describe long-term movement patterns of 1280 individually tagged adult benthivorous bream (*Abramis brama*) in a multi-lake drainage system during nine years. The movement pattern can best be described as partial nomadism, where a part of the population are neither resident nor migratory, but instead move between lakes in an unpredictable arrhythmic fashion, often with long residency in one lake before moving to the other lake. On average 15% of the tagged bream changed lake within the first year after tagging, but there was extensive variation in the amount of moving bream between years, from 0% to 37%. In total, 30% of the bream that changed lake returned to the lake of tagging after 1-3 years, but the majority did not return during the study years. Notably, movements out of lakes were significantly more in direction of the neighboring lake than away from the sister-lake system, suggesting that at least direction was not random. This opens up for important questions regarding

the mechanisms governing the patterns of nomadism. Further, since bream are important bioengineers, fluctuating densities of adult bream could cause ecological instability in lakes. Our study suggests that fish populations in inter-connected lakes in freshwater systems should not be treated as isolated units and we discuss this in relation to lake ecology and the importance for lake ecosystem management.

Introduction

Animal movement between ecosystems often occurs in predictable rhythmic patterns (Dingle & Drake 2007; Chapman et al. 2014). Such migratory movements are key events in many individual life histories and can have large effects on ecosystems (e.g. Post et al. 2008; Brodersen et al. 2011; Bauer & Høye 2014; Brodersen et al. 2015). However, individual movements between ecosystems may also occur in more seasonally or ontogenetically unpredictable arrhythmic fashions (Jonzén et al. 2011). Such dispersal-like movements are cornerstones in meta-community- and meta-population theory (Leibold et al. 2004; Hanski 1998). One such form of movement is nomadism, i.e. animals that are neither resident nor migratory, but instead move across the landscape in routes that do not repeat across years (Mueller & Fagan 2008). Even though, nomadism is a widespread phenomenon, it is highly understudied compared to other movement types (Holyoak et al. 2008; Mueller & Fagan 2008). Furthermore, previously described examples of nomadism generally concerns mammals (e.g. Fryxell et al. 2004; Singh et al. 2012) and birds (e.g. Andersson 1980; Korpimäki et al. 1987; Allen & Saunders 2002), whereas nomadism in fish has been suggested (e.g. Myers 1949; Quinn & Brodeur 1991), but rarely described in larger detail. This represents an insufficient knowledge, both in terms of understanding the dynamics of ecology and evolution of fish and in forms of management of fish populations and ecosystems, such as freshwater lakes.

Traditionally fish populations in lakes are managed as distinct entities, just as lakes have been viewed as isolated ecosystems (Forbes 1887; Hansson et al. 2013). However, it is important to acknowledge that this is far from always the case as lakes are most often connected with other lakes through in- and outlet streams, implying that lacustrine fish can distribute between lakes with potential consequences for trophic interactions and ecosystem stability. That fish move between lakes within river drainage systems is more or less given based on knowledge about fish biogeography (e.g. Olden et al. 2001) and population genetics (e.g. Stepien et al. 2009). However, actual documentation of individual movement between lakes is rare, despite several methods have

showed promise of solving this riddle, e.g. otolith microchemistry (Whitledge et al. 2006) and biotelemetry (Cooke et al. 2004). Actual documentation of individual between-lake movement patterns are however needed in order to understand its role in large scale processes, such as gene flow and ecosystem stability. Questions remain open regarding whether such between-lake movement is part of migratory patterns, unidirectional dispersal, or other movement pattern, e.g. nomadism, which may contain aspects of both migration and dispersal.

In Northern European lakes, bream (*Abramis brama*) is a common and abundant freshwater fish (Tammi et al. 1999; Kottelat & Freyhof 2007). Adult benthivorous bream are highly specialized and important ecosystem engineers with the prospect of contributing in structuring and altering freshwater lake systems. Benthivorous bream feeding activity may cause resuspension of sediment particles as well as release of nitrogen and phosphorus into the water column (Boström et al. 1982; Andersson et al. 1988; Breukelaar et al. 1994; Zambrano et al. 2001; Parkos et al. 2003; Fisher et al. 2013). Nutrient release from the sediment and resuspension leads to an increase in water turbidity due to increasing growth of algal biomass as well as an increase in dissolved particles in the water. This impoverishes growth of submerged macrophytes and effects the population sizes and size structure of planktivorous and piscivorous fish (Harper 1992; Cooke et al. 1993; Carpenter et al. 1998; Jeppesen et al. 2005). Ultimately, adult bream can therefore play a major role both for shifting lakes to a more eutrophic state and subsequently maintaining lakes in a turbid state (Parkos et al. 2003; Fisher et al. 2013). Despite the fact that benthivorous bream are important bioengineers in shallow lakes with high per capita influence of ecosystem dynamics and stability, not much is known about its spatial ecology in freshwater systems (see however Molls 1999; Lilja et al. 2003). With its capacity for individual long-distance movements (e.g. Berg 1949; Kottelat & Freyhof 2007; Lucas & Baras 2008) and high age (Kottelat & Freyhof 2007), bream may potentially occupy several lakes during their life history, which may affect local ecosystem dynamics. It is therefore highly relevant to explore if and how benthivorous bream move between lakes within a drainage system.

In this study, we describe partial nomadism of adult benthivorous bream moving between two shallow Danish lakes using a data series of nine contiguous years. We explore seasonal and daily patterns as well as the magnitude of the movements, i.e. the percentage of the populations in the

two lakes that move from one lake to the other. Furthermore, we explore return patterns, i.e. if and when bream return to the lake of first observation following a shift to another lake.

Material and methods

Study site and fish sampling

Patterns of seasonal and daily migration of bream were explored between two Danish lakes (Fig. 1). Lake Loldrup (56°29'N, 9°26'E) is a small and shallow lake (area of 0.39 km², average depth of 1.2 m). The fish community of Lake Loldrup is dominated by bream and roach (*Rutilus rutilus*), but also pike (*Esox lucius*), perch (*Perca fluviatilis*), and few pikeperch (*Sander lucioperca*) are present in the lake. Lake Viborg (56°26'N, 9°25'E) is somewhat larger and consists of two basins. The northern basin is marginally smaller and deeper (1.23 km², average depth of 7.0 m) than the southern basin (1.46 km², average depth of 3.4 m). The two basins are separated by a 50 m long and 6 m wide stream without barriers, i.e. fish are able to distribute freely among the basins. The fish community in Lake Viborg consists mainly of bream, roach, pike, perch, pikeperch, with carp (*Cyprinus carpio*) being less abundant. In both lakes, the size distribution of bream appears to be strongly bimodal (Fig. S1), with a low abundance of bream around 350 mm. We are in this study focusing on the largest size group of bream (≥ 350 mm). Lake Loldrup and Lake Viborg are connected through a 2.2 km long stream (width; range 2-6 m, slope; mean 0.02%, depth; range 0.5-1.5 m) with no physical obstructions (Viborg Municipality, 1981). Moreover, there is an inlet stream to Lake Loldrup and an outlet stream from the southern basin of Lake Viborg (Fig. 1).

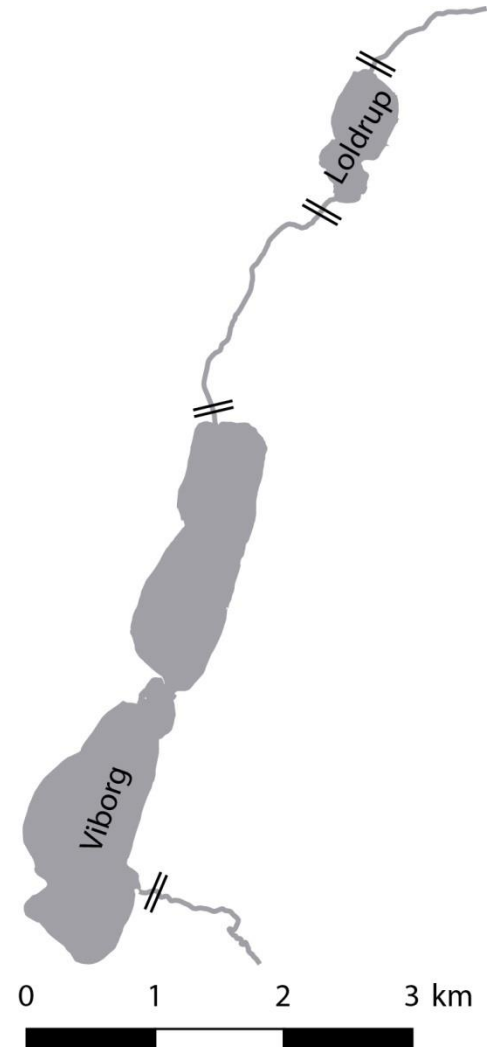


Figure 1: Lake Viborg and Lake Loldrup and the position of the passive integrated transponder (PIT) stations (black lines).

PIT tagging and monitoring of movements

From 2008 to 2016, an average of 71 adult bream (ranging between 22-155 per year) (≥ 350 mm in length; 447.0 ± 44.1 mm, mean total length \pm SD) were tagged annually with Passive Integrated Transponder (PIT) tags resulting in a total of 1280 bream (Table 1). Bream for tagging were caught

in both lakes in late September/early October (water temperature 8.7-15.5°C) using seining and gill nets set for a short duration of time (maximum 2 hours) to minimize gill net damage on the fish. Upon capture, bream were anaesthetized with benzocaine (20 mg L⁻¹) and afterwards measured (total length to nearest 1 mm) and weighed (wet body mass to nearest 1 g). A 23 mm PIT tag (Texas Instruments, RI-TRP-RRHP, half duplex, 134 kHz, 0.6 g mass in air) was inserted into the body cavity through a small incision on the ventral-left side of the body posterior to then ventral fin. The tagging incision was left to heal without suture closure to avoid infections (Skov et al. 2005). Surgical implants were performed by an experienced fish surgeon in accordance to the guidelines described in permission (2012-DY-2934-00007/BES) from the Danish board for use of experimental animals.

Movement of tagged bream entering and leaving Lake Loldrup and Lake Viborg, as well as movement between the lakes was monitored throughout the study period. Four sets of two loop-shaped antennas, each covering the entire cross section of the stream and situated 3-5 meters from each other were placed close to the inlets and outlets of Lake Loldrup and Lake Viborg, respectively (Fig. 1). Using two sequential antennas enabled determination of bream swimming direction.

Data treatment

Once a tagged bream passed an antenna, the PIT-tag energized and emitted a unique code, which was recorded and stored together with date and time. Evaluations of diel and seasonal patterns of inter-lake movements were based on inspections of time of first registration on the PIT antenna closest to the lake in which bream was PIT tagged and the subsequent last registration on the PIT antenna closest to the neighboring lake. These two “end points” also made it possible to estimate travel time between the two lakes. Some fish returned to the lake they were tagged in during the study period (2008 to 2016). For these individuals we calculated the time spend in the neighboring lake before return movement. The annual percentage of bream that moved to the neighboring lake was establish as the share of the bream, tagged in a given year, that moved from one lake to the other from the time of tagging (September or October) until time of tagging the following year, i.e. normally 12 months. Likewise, the annual share of tagged bream visiting the inlet stream of Lake Loldrup or the outlet stream of Lake Viborg, i.e. bream that were detected on the antennas furthest away from the lake basin were calculated.

All statistical analyses were conducted in SPSS, v. 23.0. (SPSS Inc., Chicago, IL, USA) and the statistical computing program R (R Core Team, 2016).

Results

Proportion and direction of moving individuals

There were substantial, but arrhythmic movements between the two lakes during the nine years of monitoring (Table 1, Fig. 2). Averaged across study years, 15.0% of all tagged bream moved between lakes from the time of tagging in autumn until time of tagging the following year. A slightly higher percentage of bream moved downstream from Lake Loldrup to Lake Viborg (15.5% of all bream tagged in Lake Loldrup, Table 1) than upstream from Lake Viborg to Lake Loldrup (14.6% of all bream tagged in Lake Viborg, Table 1). The share of movers varied in the different years and between lakes, illustrated by a

significant interaction term between release system (lake) and year (logistic regression; $\chi^2 = 46.9$, $p < 0.001$). The magnitude of upstream movements from Lake Viborg to Lake Loldrup varied between years from 0% (bream tagged in 2010 and 2012) to 37% (bream tagged in 2008) (Table 1, Fig. 2). Likewise, the magnitude of annual downstream movements, i.e. from Lake Loldrup to Lake Viborg varied from 0% (bream tagged in 2011) to 24% (bream tagged in 2014 and 2015) (Table 1, Fig. 2). Movement of bream appeared to be specifically directed towards the neighboring lake, as there was only negligible movement into the tributary of the upstream lake (Lake Loldrup) and into the outflow of the downstream lake (Lake Viborg). Specifically, fish tagged in Loldrup were more likely to move downstream compared to bream from Lake Viborg, which were more likely to move upstream (Pearson χ^2 -test; $\chi^2 = 167.0$; $p < 0.001$) (Fig. 2).

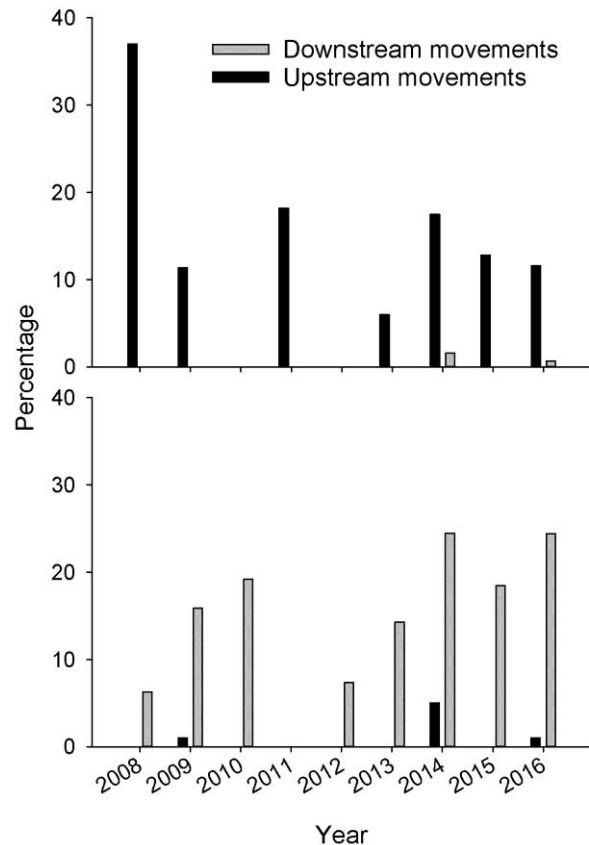


Figure 2: Direction of movement, i.e. the percentage of the tagged bream in a given year moving upstream or downstream from the lake within the first 12 months, for bream tagged in Lake Viborg (top) and Lake Loldrup (bottom).

Table 1: Bream (> 350 mm) sampled and tagged from 2008 to 2016 in Lake Loldrup and Lake Viborg. Number of tagged bream, number and percentage of moving individuals (the year following tagging), number and percentage of returners (at any point in time during the study period), mean retention time in the neighboring lake for returners (and SD).

Release system	Tag year	Direction	# tagged	# moved	# returners	Retention time mean (days)	Retention time SD (days)	Movers (% of tagged)	Returners (% of movers)
Loldrup	2008	Downstream	32	2	1	0.03		6.3	50.0
Viborg	2008	Upstream	119	44	14	734.6	843.8	37.0	31.8
Loldrup	2009	Downstream	82	13	0			15.9	0.0
Viborg	2009	Upstream	97	11	8	300.5	635.7	11.3	72.7
Loldrup	2010	Downstream	73	14	3	173.6	12.1	19.2	21.4
Viborg	2010	Upstream	52	0	0			0.0	
Loldrup	2011	Downstream	32	0	0			0.0	
Viborg	2011	Upstream	22	4	1	743.9		18.2	25.0
Loldrup	2012	Downstream	109	8	6	433.8	300.1	7.3	75.0
Viborg	2012	Upstream	23	0	0			0.0	
Loldrup	2013	Downstream	42	6	5	466.5	181.6	14.3	83.3
Viborg	2013	Upstream	117	7	3	271.4	212.0	6.0	42.9
Loldrup	2014	Downstream	90	22	5	401.0	173.2	24.4	22.7
Viborg	2014	Upstream	63	11	7	121.5	176.6	17.5	63.6
Loldrup	2015	Downstream	92	17	2	307.5	37.6	18.5	11.8
Viborg	2015	Upstream	39	5	3	126.6	180.1	12.8	60.0
Loldrup	2016	Downstream	41	10	0			24.4	0.0
Viborg	2016	Upstream	155	18	9	6.1	7.6	11.6	50.0

Seasonal and diel movement patterns

On average, the majority of bream movements from Lake Viborg upstream to Lake Loldrup (67.8%) occurred during the month of May (Fig. 3). In contrast, downstream movements from Lake Loldrup to Lake Viborg occurred more evenly over the year (Fig. 3), with a peak in September (39.2%). Bream tagged in Lake Viborg largely initiated their inter-lake movement during darkness (Fig. 4A). Bream tagged in Lake Loldrup initiated inter-lake movements more often during daylight than bream from Lake Viborg (Pearson χ^2 -test; $\chi^2 = 33.0$; $p < 0.001$; Fig. 4C). Likewise, bream tagged in Lake Viborg also completed their upstream movements into Lake Loldrup during the dark (Fig. 4B). Still, as it was the case for upstream movements (from Lake Viborg to Lake Loldrup), the downstream movements were also primarily completed in darkness during the night (Fig. 4D). There was no significant difference between lake of origin in whether bream completed their inter-lake movement during daylight or not (Pearson χ^2 -test; $\chi^2 = 3.11$; $p = 0.078$).

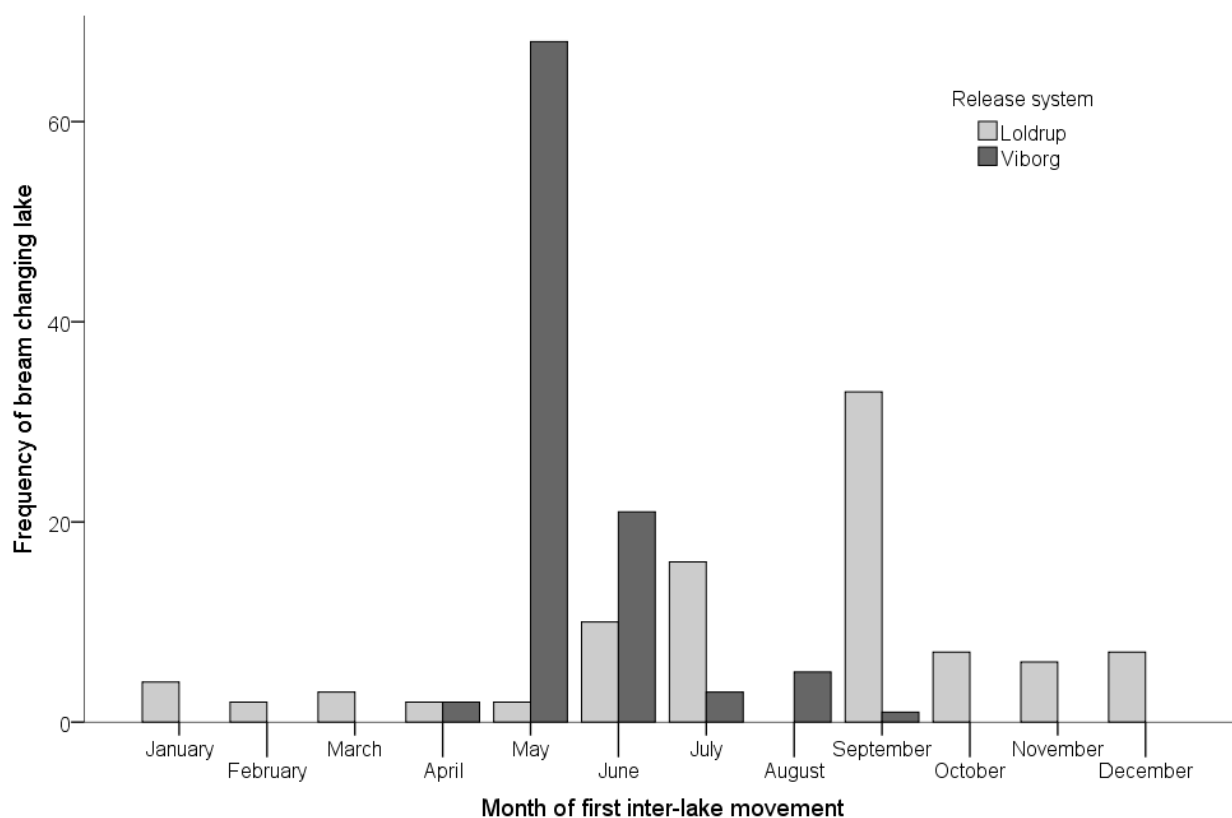


Figure 3: Frequency of bream (≥ 350 mm, tagged in September/October) changing lake. Black bars show percentage of bream (all study years pooled) moving upstream from Lake Viborg to Lake Loldrup and grey bars show percentage bream moving downstream from Lake Loldrup to Lake Viborg.

Swimming speed during movement

Travel time for bream swimming upstream from Lake Viborg to Lake Loldrup was 5.5 ± 7.1 hours (mean \pm SD), corresponding to an average ground speed of 0.11 m s^{-1} . However, there seemed to be seasonal variation as travel time during spring (April, May, and June; 1.9 hours (0.32 m s^{-1})) was 73.0% faster than in the winter months (December, January, and February; 7.05 hours (0.09 m s^{-1})). The average downstream travel time was 6.4 ± 7.5 hours (mean \pm SD), corresponding to an average ground speed of 0.095 m s^{-1} .

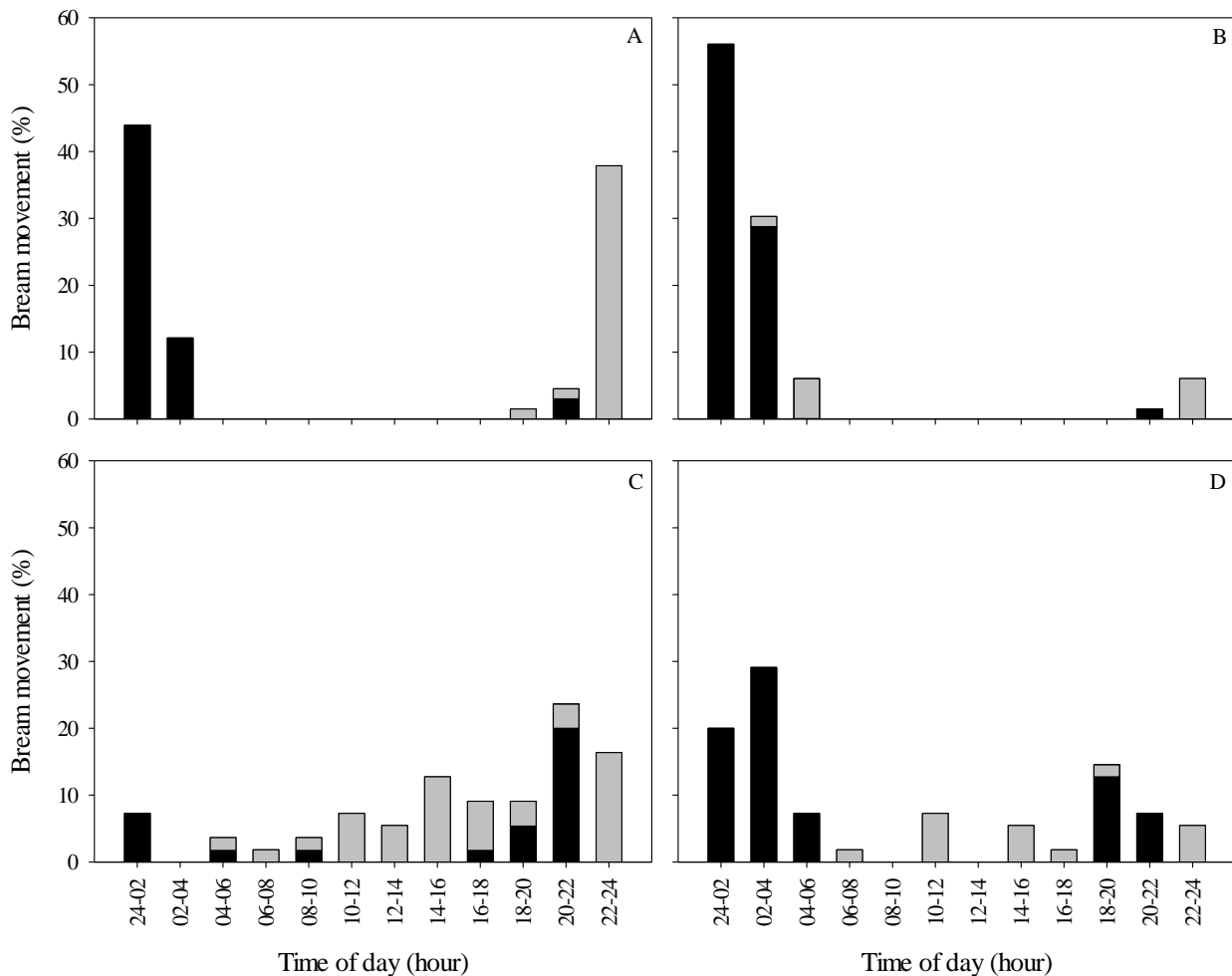


Figure 4: A and B represents bream moving from Lake Viborg, C and D represent bream moving from Lake Loldrup. Black bars in A and C show percentage of bream initiated their migration in the dark and grey bars show percentage of bream initiated their migration in sunlight. Black bars in B and D represent migration completed in the dark while grey bars represent migration completes in sun light

Retention time and return rate

35% of the bream that changed lake (4% of all tagged bream) returned to the lake, in which they were tagged within the study period. There was large variation between individuals and years with regards to the time spend in the neighboring lake before return migration (Table 1) and varied between 69 days up to 6 years. There was also substantial variation in retention time between lakes (Table 1) Viewed across all study years, a higher share of bream tagged in Viborg returned after visiting Lake Loldrup (45%) compared to bream tagged in Lake Loldrup visiting Lake Viborg (24%) (Pearson χ^2 -test; $\chi^2 = 8.47$; $p < 0.01$). Moreover, 23.4% of the inter-lake moving bream moved more than once to the neighboring lake.

Discussion

In this study, we described benthivorous bream movements between two connected neighboring lakes using a nine-year long time series. Furthermore, we provided valid evidence that a part of the benthivorous bream population frequently move between the two lakes in an arrhythmic and no predictable fashion, and we argue that these patterns are best described by nomadism. Whereas dispersal and migration are general terms to describe movement, nomadism can be considered as a specific movement pattern (Holyoak et al. 2008) including elements from both dispersal and migration terminology. Most often nomadism has been related to ungulates or birds however, the definition of nomadism has varied (Mueller & Fagan 2008). Most definitions include that the movement patterns are unpredictable in time and space. Indeed, the movements of bream during the nine years study period were arrhythmic and unpredictable in time as illustrated by the variation in the proportion of movers between the lakes and years, the variation in the share of returners, and the variation in retention time between returners and between lakes. Moreover, it was unpredictable in space as some individuals travelled between lakes more than once. Finally, not all of the population participated in the between-lake movements, i.e. some individuals were resident. Hence, we propose that bream can be considered partial nomads. To our knowledge, this term has not been used before to describe fish movement patterns.

In line with the definition given above, there was large variance between years in the extent of nomadism, and in some years as many as 35% of the adult population may change lake. Even though cyprinids are known to be migratory, relatively little is known about their long distance movements and localized activity patterns (Mills 1991; Smith 1991), and this is to your knowledge

the first study to, in detail, monitor movements of bream between two lakes on an individual level and over a substantial time period. However, other studies have investigated movements of cyprinids, including bream, in reservoirs, tributaries, and rivers (Lucas & Batley 1996; Hladík & Kubečka 2003; Skov et al. 2011; Skov et al. (unpublished)). Combined, the present knowledge demonstrate that bream movement life history is complex and may contain changes with ontogeny from seasonal migration in younger individuals (Skov et al. 2011) and partial nomadism in large adults, which fits well into the movement ecology paradigm (Nathan et al. 2008).

Like migration, nomadism may often occur with certain seasonality (Jonzén et al. 2011). The movements of bream upstream from Lake Viborg to Lake Loldrup occurred primarily in spring, while the months with highest frequency of movements downstream from Lake Loldrup to Lake Viborg was during fall i.e. September and October (Fig. 3). According to the theory, nomadism occurs when resources fluctuate irregularly on a multi-year timeframe over large geographic areas (Mueller & Fagan 2008). Since resources also could relate to available spawning sites, a possible reason for the high movement rate in spring from Lake Viborg to Lake Loldrup could be associated with a search for suitable spawning grounds. Lucas & Batley (1996) found that the riverine cyprinid fish species (*Barbus barbus*) performed seasonal movements migrating upstream the river in spring to spawn and moving downstream after spawning in fall and winter. Generally, we observed a similar movement pattern of benthivorous bream moving upstream in spring and downstream during fall/winter. However, the mean retention time for returning bream was on average longer than five month from spring to fall and variations in movement patterns were highly individual. This indicates that even though the upstream movement to Lake Loldrup could be associated with spawning, many of the migrating bream do not overall move back to Lake Viborg the following fall or winter. Moreover, the majority of the individuals that moved upstream stayed in Lake Loldrup until the end of the research period, while other individuals have in fact multiple movements, i.e. return to Lake Viborg a year or more after their first moved to Lake Loldrup. Even though movements and migrations from Lake Viborg to Lake Loldrup were most intense in May and June and hence could relate to spawning (e.g., Mills 1991; Lilja et al. 2003), we did not observe the same patterns when exploring bream moving from Lake Loldrup to Lake Viborg. Here the movements take place in all months, although mostly in autumn. This suggests that other mechanisms in addition to search for spawning areas could be in play as well such as fluctuations in food availability. To summarize, the movement patterns of bream observed in this study were complex

and indeed unpredictable and best explained as nomadism movement patterns. Future studies should focus on collecting thorough information about fluctuations in spawning area availability or feeding resources to explore the mechanisms behind these nomadism movement patterns further.

A key character of fully nomadic species is that they at any given site may appear in large numbers one year and then not be seen for multiple years at that site (Jonzén et al. 2011), which we would expect to drastically disrupt local food web structure. Similarly, we suggest that also for partially, in contrast to fully, nomadic species, ecosystem effects may occur as a result of abrupt changes in local densities in coupled ecosystems. Given that a large proportion of a bream population sometimes move from one lake to another, as shown in this study, the fish community within a lake can change drastically within a short period. This can have important effects on the lake ecosystem, especially if the moving species is an important bioengineer, as is the case in adult benthivorous bream. Many shallow lakes, including Lake Loldrup, occasionally shift between alternate stable states with either clear water and high macrophyte biomass or turbid water with high phytoplankton biomass (Scheffer et al. 1997; Carpenter et al. 1999). In fact, although only anecdotally described, Lake Loldrup have over the last 15 years a few times alternated between a clear water state with high density of submerged macrophytes, and a turbid state with low Secchi depths and no submerged macrophytes. We therefore predict that the movement of adult benthivorous bream may affect the shift between alternate stable states in shallow lakes. This would have importance for future practice of lake restoration and specifically for biomanipulation, where benthivorous and planktivorous fish are removed to achieve a clearer water conditions in eutrophic lakes. However, this study opens up for the possibility that removal effort can be counteracted by immigration from neighboring lakes. Understanding mechanisms of bream movements between neighboring lakes can add to our understanding why effects of biomanipulation rarely last for long (Søndergaard et al. 2007). We therefore suggest that future biomanipulation attempts in lakes take the potential of immigration of bream from neighboring lakes into account.

Diel movement patterns of cyprinids in streams have previously been described as being variable between species and seasons (Hohausová et al., 2003; Skov et al., 2008; Nunn et al., 2010). This study add to this complexity by showing that diel patterns can, within a single species, also depend on movement direction in a stream, i.e. bream initiated and completed their upstream movements mainly during dark (See Borcheding et al. 2002, for similar diel patterns of stream movements of

adult bream), while downstream movements were more evenly distributed during the day. At this stage, we can only speculate about reasons for this variation, but it could relate to inter-lake variation in foraging patterns and/or predation risk, i.e. factors that often determines whether freshwater fish are diurnal or nocturnal at any particular time and place (Reebs 2003). However, it should be noted that adult benthivorous bream have outgrown predation risk from far most predators, such as pike and cormorants (e.g. Skov et al., 2011; Skov et al., 2014), and therefore reduction in predation risk, e.g. by moving during dark, maybe less likely as a driver of the timing of movement between lakes.

The mechanisms controlling the patterns of partial nomadism observed for bream in this study is still unknown. However, the non-randomness in swimming direction suggests that spatial memory play an important role, which is in line with many other types of animal movement (Fagan et al. 2013). Bream are gregarious organisms (Kottelat & Freyhof 2007) and the strong directionality would suggest social transmitted knowledge. Nonetheless, this was not possible to test in this study, since only a small proportion of the whole bream population was tagged and tracked. Hence, it was not obtainable to monitor which and how many untagged individuals there were moving along with the tagged bream. Finally, it has been suggested that nomadism should be supported by temporally unpredictable broad-scale landscape dynamics. We suggest that future studies should be designed to further illuminate these aspects of partial nomadism in fish.

Acknowledgements

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Supplementary material

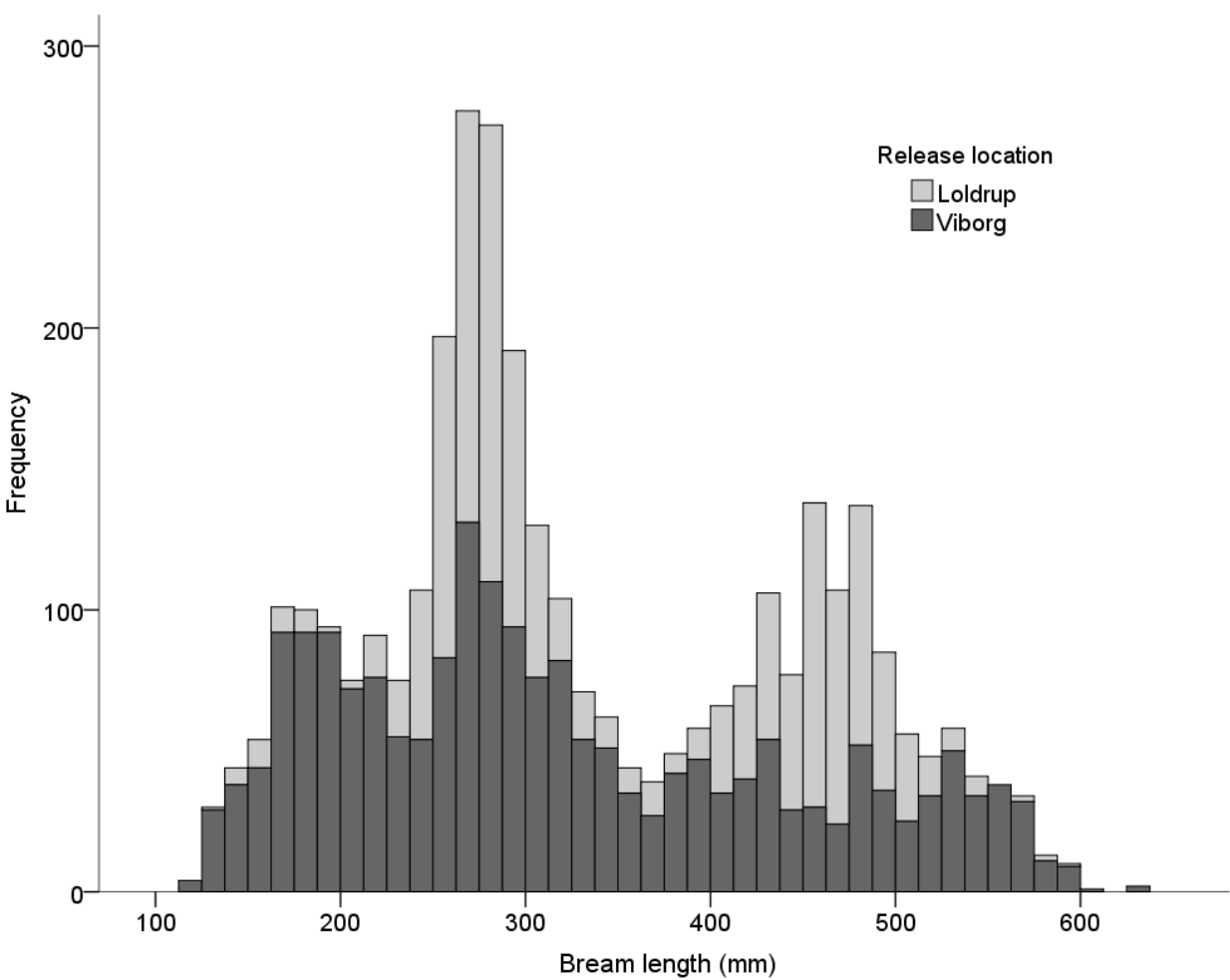


Figure S1: Size distribution of all tagged bream > 110 mm caught in Lake Loldrup (light grey bars) and Lake Viborg (dark grey bars) between 2008 and 2016.

PAPER IV

Biomanipulating streams: a supplementary tool in lake restoration



Biomanipulating streams: a supplementary tool in lake restoration

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Abstract

Removal of cyprinid fish is a widely used biomanipulation tool to transform turbid eutrophic lakes into a clear-water state, thereby increasing biodiversity. We evaluate the extent to which removal of cyprinids from streams can be a supplementary tool to this. Cyprinids often aggregate in lake inlet/outlet streams during winter migrations, and since stream aggregation sites contain less volume than lakes, removal of fish in this habitat may be more cost-effective as compared to lake fishing. In two consecutive years, we annually removed up to 35% of the dominant cyprinids from an inlet stream to a lake system, and argue that this could be easily increased with a more targeted fishing effort. At the same time, we monitored the migration patterns of individual fish to evaluate species- and length-specific variation in migration propensity to explore how this relates to effective fish removal. Large benthivores had lower migration propensity than smaller planktivores why stream fishing should be complemented with traditional in-lake fishing methods. As a rule of thumb, stream fishing is most efficient when lake water temperatures are 2-6°C. Prior to implementing fish removals from streams as a biomanipulation tool, the potential evolutionary consequences of the targeted removal of migratory phenotypes should be considered.

Introduction

Freshwater ecosystems are affected by anthropogenic activities worldwide (Brönmark & Hansson, 2002), such as exposure to increased nutrient loadings from e.g. land use and inefficient sewage treatment. High nutrient inputs into lakes can have substantial eutrophication effects, frequently leading to reduced biodiversity, altered community composition, and shifts between alternative stable states, from clear-water to turbid water states (Scheffer, 1998; Hansson et al., 1998; Schindler, 2006). The change to the turbid state involves a reduction of piscivorous fish and submerged macrophytes and a concomitant increase in benthivorous and zooplanktivorous fish and recurrent algal blooms. This turbid, undesired state is stabilized by internal feed-back loops and so persists even when nutrient load is reduced (Hansson et al., 1998). Such shifts in system composition and function are generally in conflict with water directives and ecosystem services, and eutrophic lakes are regularly targeted by management incentives to restore lake systems (Moss et al., 2002). Lake restoration can be approached by, for instance, reducing nutrient loads and/or by biomanipulation, i.e. reduction fishing of zooplanktivorous and benthivorous fish (Hansson et al., 1998; Søndergaard et al., 2007a, 2008). Biomanipulation of lakes by removing zooplanktivorous and benthivorous fish aims to alter the fish community composition and thereby the structure of the

whole lake ecosystem through changes in cascading trophic interactions. The reduction of zooplanktivorous fish is expected to reduce zooplankton predation, and hence, increase overall survival and enhance the potential for zooplankton to reduce phytoplankton biomass, and ultimately increase water transparency and opportunities for macrophyte establishment and piscivores foraging success (Shapiro, 1978; Hansson et al., 1998). Reductions of benthivorous fish also favor the shift towards the clear-water state through reduced sediment re-suspension (Anderson et al., 1978; Breukelaar et al., 1994). Biomanipulation can be performed by e.g. selective trawling and/or fyke netting for zooplanktivorous and benthivorous fish, but up to 50-80% of their biomass, or more than 200 kg/ha, has to be removed, often repeatedly, to obtain and maintain the desired ecosystem effects on targeted lakes (Hansson et al., 1998, Olin et al., 2006; Søndergaard et al., 2008). Such large-scale fishing is labor intensive and costly, partly due to the unpredictable spatio-temporal distribution of targeted zooplanktivores/benthivores and, hence, complementing capture techniques and more efficient fish-removal methods are desirable to increase the success of biomanipulation efforts.

When performing a biomanipulation it is important to recognize that different functional groups of fish play different roles in maintaining lakes in a turbid state and it is desirable to target all of these groups. One important functional group is zooplanktivorous fish, often (but not exclusive to) the youngest age classes of cyprinid species, such as roach (*Rutilus rutilus*), bream (*Abramis brama*) and white bream (*Blicca bjoerkna*). Another important group is benthivorous fish, such as large bream, which resuspend the sediment because of their feeding behavior and thereby increase turbidity and release nutrients fixed in the sediment (Anderson et al., 1978; Breukelaar et al., 1994). Fishing in connection with biomanipulation efforts generally has long-term effects on densities of large bodied benthivores, especially bream, but has been less effective in controlling smaller bodied zooplanktivores, such as roach (Søndergaard et al., 2008). Hence developing techniques that increase capture success and reduce capture effort for such zooplanktivores is critical to ensure biomanipulation success and efficiency.

Many zooplanktivorous and benthivorous cyprinid fish species perform seasonal mass migrations, leaving their natal lakes during autumn and migrating into connected streams where they aggregate during winter to return to the lake the following spring (Skov et al., 2008). Seasonal changes in predation risk and growth opportunity in the lake and stream habitats dictate the seasonal migration patterns since fish leave lakes when the lake predation to growth ratio exceeds that of connected streams during autumn (Brönmark et al., 2008). As up to 80% of individual fish within cyprinid

populations leave the lake during winter (e.g. Skov et al., 2010) and may stay out of the lake for more than half of the year (e.g. Skov et al., 2008; Skov et al., 2010), fish migratory behavior is important to consider when performing biomanipulation as it opens up for interesting possibilities for cost-efficient fish removal of dense aggregations of zooplanktivores and benthivores in streams. Here, we investigate if removing cyprinids from streams connected to their home lake during the winter migration period could be an efficient, complementary method to lake fishing in biomanipulation efforts. We do this by 1) quantifying seasonal migration patterns of common cyprinids belonging to different functional groups, i.e. roach, common bream, and white bream, and 2) performing fish reductions by electrofishing in a lake inlet stream during two consecutive years. The results are discussed in light of cost effectiveness of different fishing methods involved in biomanipulations, practical considerations, i.e. how to optimize stream fishing efficiency, and potential evolutionary consequences.

Methods

Study site

The study took place in Lake Søgård (55°25'N, 9°19'E), a small, eutrophic, and shallow lake (area 0.26 km², average depth 1.6 m, mean summer Secchi depth 0.4-1.1 m, mean summer phosphorus concentration 0.366 mg P L⁻¹). The fish community is numerically dominated by roach and perch (*Perca fluviatilis*), with common bream, rudd (*Scardinius erythrophthalmus*), white bream, pike (*Esox lucius*), and eel (*Anguilla anguilla*) as subdominant species (Grünfeld, 2003). Lake Søgård has an inlet and an outlet stream, and previous investigations have shown that 40–70% of the cyprinid fish (especially roach (Skov et al., 2010), bream (Skov et al., 2011), and white bream (Skov unpublished)), use the streams as overwintering habitats.

PIT tagging and monitoring of seasonal fish migration

Fish for PIT-tagging (TIRIS Passive Integrated Transponder, Texas Instruments, RI-TRP-RRHP, half duplex, 134 kHz, 23.1 mm long, 3.85 mm diameter, 0.6 g in air) were captured by various methods, including electrofishing, beach seining, and gill netting in late September of 2013 and 2014. Gill nets were set and emptied within 2 hours to minimize the impact of gill net entanglement on fish health and condition. After capture, fish were individually weighed to the nearest 0.1 g, measured to the nearest millimeter (total length), and tagged according to Skov et al., (2005) by surgically implanting a PIT tag into the stomach cavity of the fish. An evaluation of PIT-tag

marking techniques has shown that the method causes no significant effect on fish well-being, including body condition (Skov et al., 2005). In total 291 and 360 roach, 210 and 138 bream, and 36 and 14 white bream were tagged in 2013 and 2014, respectively. After recovery from tagging, fish were released approximately in the center of Lake Søgård. Surgical implants were performed by an experienced fish surgeon in accordance to the guidelines described in permission (2012-DY-2934-00007/BES) from the Danish board for use of experimental animals.

In order to evaluate the proportion of cyprinid fish that migrated during winter, we monitored migration of tagged roach, bream, and white bream between the lake and the inlet and outlet streams by passive biotelemetry, i.e. a PIT-tag antenna system (Skov et al., 2005; Skov et al., 2008). Two loop-shaped antennas, each covering the entire cross section of the stream, were placed 3–5 m apart in the inlet (15 m upstream the lake) and the outlet streams (150 m downstream the lake, as outlet topography did not allow installation of antennas closer to the lake). The use of two sequential antennas enables determination of fish swimming direction. The antenna recording frequency were 5 energize/receive cycle's s^{-1} . The antennas energize the PIT tags in passing fish, and the PIT tag emits a unique code that is stored together with date and time on memory hardware in the antenna system. Once a day data are transferred via GPRS to a server, where it is stored for later analysis. This enables us to estimate the percentage of tagged fish that were present in the inlet or outlet at any given time. Here we present migration data, i.e., daily average percentage of tagged fish outside the lake from the winter seasons (late September until mid-May, when return migration to the lake had ended) 2013/2014 and 2014/2015. However, since previous studies have shown that cyprinids in Lake Søgård mainly migrate to the inlet stream during their winter migration (Skov unpublished data) the stream fishing were therefore focused on this stream and, hence, we only present migration data from the inlet stream.

Stream fishing

During the winters 2013/2014 and 2014/2015 cyprinid fish were removed from the lower 400-500 meters of the inlet stream by electrofishing. This was done from a small boat or by wading, with one person fishing and netting and another person assisting. Non-cyprinid fish, such as perch and pike, were released back into the stream. The cyprinid fish were killed using an overdose of benzocaine, pooled in large bins and brought back to the laboratory. On the following day cyprinid fish were sorted according to species and fish ≥ 20 g, i.e. potentially tagged fish. PIT-tagged fish

were then counted to form a basis for capture-recapture estimates of fish ≥ 20 g. The total biomass of the catch of fish ≥ 20 g was in 2013/2014 established by manually sorting the catch into two bins (i.e. fish < 20 g and fish ≥ 20 g) and weighing these separately. In 2014/2015, total biomass of fish ≥ 20 g was estimated by weighing a random collected subsample of individuals (Supplementary table 1) from the total catch from which the biomass-share of fish ≥ 20 g was established and subsequently multiplied with the biomass of the total catch. The average individual weight of fish ≥ 20 g in the catch, which was used in the mark recapture calculations, was in 2013/2014 estimated from a random sample (minimum 60 individuals, if possible) from the pools of fish ≥ 20 g, which were individually weighed to the nearest 0.1 g and measured to the nearest millimeter (total length). In 2014/2015 it was estimated by measuring length and weight of all fish ≥ 20 g in the subsample from the total catch (containing also fish < 20 g) mentioned above.

Temperature monitoring

Lake water temperature was monitored in the lake outlet by Tidbit® (Hobo, Massachusetts, USA) storage loggers, logging temperature once every hour throughout the study period.

Data processing and statistics

To identify time-periods suitable for fishing in the stream and to illustrate year-to-year and species-specific differences in migration propensity, we plotted the daily proportion and running mean (width of moving window = 10 days) of fish in the stream (26th September to 15th May) for all three tagged species together with the average daily temperature. Further, we calculated the average daily proportion of the population that was in the stream in the period 1st November to 1st April.

Size-specific patterns of migration propensity were explored for each species using a Bernoulli distributed generalized linear model (GLM, logit-link) with migration (yes/no) as dependent variable and length at tagging, year, and the interaction term between length and year as predictors.

To estimate the species-specific population proportions that were removed, we used capture mark recapture methodology, i.e. the adjusted Pedersen estimate (Ricker, 1975) (eqn. 1)).

$$N = \frac{(S_1+1)(S_2+1)}{M+1} \quad (\text{eqn. 1})$$

where,

N = estimated population size (numbers), S_1 = number of initial PIT tagged fish ≥ 20 g, S_2 = number of caught fish ≥ 20 g (minimum size at PIT tagging), and M = number of recaptures, i.e. all PIT tagged fish caught during stream fishing.

Since we did not count all individuals that were sampled during the stream fishing, but only weighed total catch, we subsequently calculated (S_2) by multiplying the total biomass removed per year (biomass from all fishing sessions pooled) with the average individual weight (W_{avg} in Table 1) from all fishing sessions. The latter was found by taking the mean of the average individual weights (Ind. $W(g)$ in supplementary Table 1) found at each stream fishing session. Further, 95% confidence interval was calculated (eqn. 2) (Ricker, 1975).

$$CI_{95\%} = \pm 1.96 \sqrt{\frac{N^2(S_2 - M)}{(S_1 + 1)(M + 2)}} \quad (\text{eqn. 2})$$

Results

Seasonal cyprinid migration

Migration of roach, bream, and white bream into the inlet stream occurred in both winter seasons (Fig. 1). Overall migration patterns were comparable across years, but with differences in migration timing and intensity between species. In both seasons, migration into the inlet was initiated in late October with a marked peak in migration intensity, i.e. the proportion of migrants, in late November, when temperatures dropped below 6°C (Fig. 1). Return migration to the lake occurred in March to April for all three species (Fig. 1).

The proportion of bream in the inlet was lower compared to that of roach in both years, and in 2013/2014 it was also lower than for white bream (Fig. 1). The share of migrating fish in the populations, i.e. fish that at some point during winter migrated to the inlet and stayed for a minimum of 24 hours, was 32% (2013/2014) and 28% (2014/2015) for bream, 61% (2013/2014) and 43% (2014/2015) for white bream and 60% (2013/2014) and 82% (2014/2015) for roach. The maximum proportion of fish present at any point during the two winters was 58% and 73% of the tagged roach, 61% and 43% of the tagged white bream, and 29% and 44% of the tagged bream (Fig. 1). The same pattern is observed when calculating the average percentages of the populations that used the stream habitat from 1st November to 1st April, with 40% and 55% for roach, 44% and 28% for white bream, and 16% and 25% for bream in the two seasons, respectively, i.e. the proportion of bream in the inlet was generally lower than the other two species.

*Table 1: Species-specific total biomass removed and calculated number of individuals removed (biomass removed/the average individual weight (W_{avg})) in seasons 2013/2014 and 2014/2015. W_{avg} is the average of all mean individual weights found at each biomanipulation fishing session (Ind. W . in supplementary table 1). Total number of marked fish (S_1), number of recaptures in the inlet (M), initial lake biomass, and the percentage reduction in total biomass including 95% confidence intervals is also presented. *Note that the low number of recaptures of bream and white bream in 2014/2015 introduce potential bias to recapture calculations why these should be interpreted with care (e.g. Ricker 1975).*

Year	Species	Biomass removed (kg)	W_{avg} (kg)	Individuals removed (S_2)	Individuals PIT tagged (S_1)	Recaptured (M)	Initial lake biomass (kg) ($\pm 95\%$ conf.)	Biomass reduc. (%) ($\pm 95\%$ conf.)
2013/2014	Roach	567	0.04	13317	291	77	2122 (1658-2586)	27 (22-34)
2013/2014	White	50	0.05	866	36	12	143 (71-214)	35 (23-71)
2013/2014	Bream	43	0.13	324	210	9	904 (401-1407)	5 (3-11)
2014/2015	Roach	348	0.04	8064	360	36	3398 (2334-4462)	10 (8-15)
2014/2015	White	17	0.09	195	14	2*	88 (12-164)	20 (7-100)
2014/2015	Bream	16	0.10	157	138	3*	587 (125-1048)	3 (2-14)

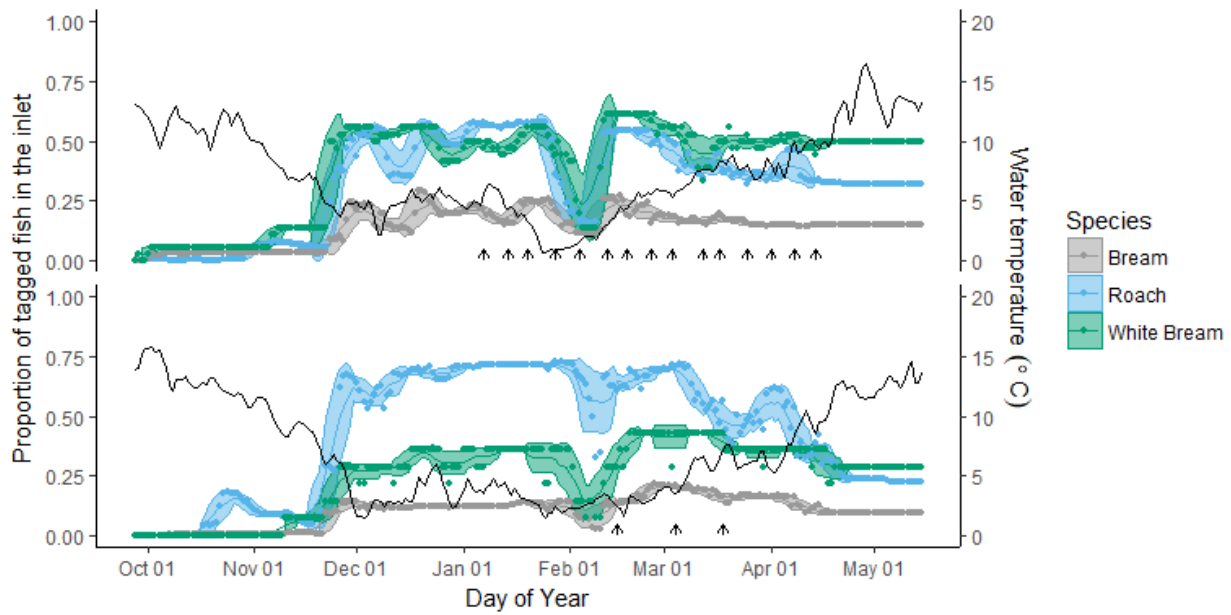


Figure 1: Proportion of tagged roach, bream, and white bream in the lake inlet in 2013/2014 (top) and 2014/2015 (bottom). Points show raw data, lines and ribbons indicate running mean \pm SD. Black lines indicate daily mean water temperature. Arrowheads show dates of biomanipulation.

The propensity to migrate varied with body length for all three species. For roach, the propensity to migrate increased with size (Fig. 2B & C; GLM, $p < 0.001$) whereas in both bream (Fig. 2D & E; GLM, $p < 0.001$) and white bream (Fig 2A; GLM, $p < 0.05$) migration propensity decreased with size. For white bream the number of tagged individuals in 2014/2015 was too low (14) for this analysis. The interaction term between length at tagging and year was non-significant for both roach and bream (GLM, $P > 0.05$ for both).

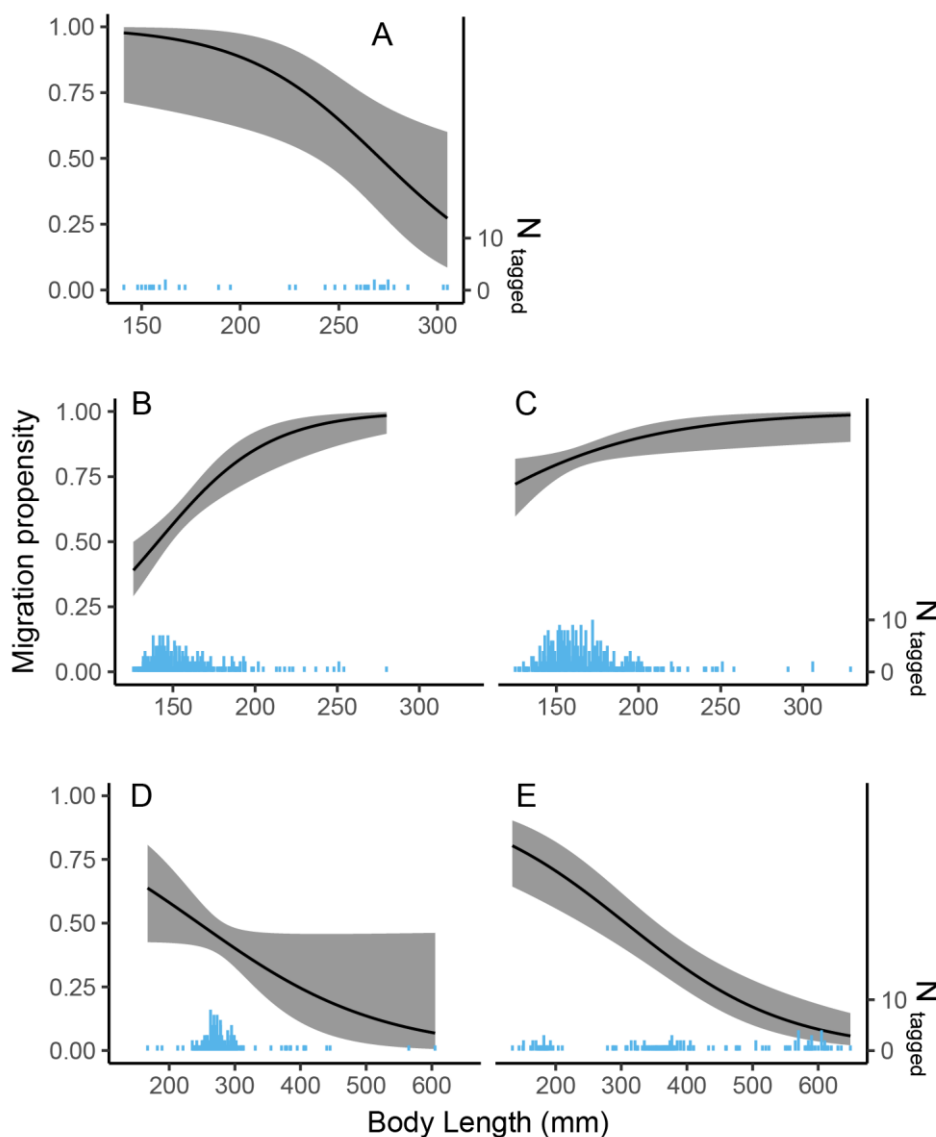


Figure 2: Length dependent migration propensity of white bream (A), roach (B & C), and bream (D & E) in 2013/2014 (left column) and 2014/2015 (right column). Lines and shaded areas are model predictions \pm 95 % confidence intervals. Blue vertical bars indicate number of tagged individuals at each length (mm). No white bream data from 2014/2015 is presented due to low number of tagged individuals.

Stream fishing

In winter 2013/2014 a total of 15 stream fishing sessions were conducted between January 7th 2014 and April 14th 2014 (Fig 1, Supplementary table 1), resulting in the removal of a total of 43 kg bream, 50 kg white bream, and 567 kg roach. Based on the capture mark-recapture estimates this corresponds to a removal of 5% bream, 35% white bream, and 27% roach of the populations of fish larger than 20 g (Table 1).

In winter 2014/2015 three stream fishing sessions were conducted between 19 February and 18 March (Fig 1, Supplementary table 1). A total of 17 kg bream, 18 kg white bream, and 348 kg roach were removed corresponding to 3%, 20%, and 10% of the populations (fish larger than 20 g),

respectively (Table 1). It should be noted that the low number of bream and white bream recaptures results in less accuracy of the estimates (Ricker, 1975), why only estimates from 2013/2014 are discussed for bream and white bream.

Each fishing session took in total a maximum of 3 hours (108.3 ± 46.4 minutes (mean \pm SD)), excluding transportation, and normally involved two persons. In 2013/2014 we therefore used a maximum of 90 man hours in fishing, whereas in 2014/2015 only 18 man hours were used during the three stream fishing sessions.

Discussion

This study demonstrates the potential of performing efficient reduction fishing by taking advantage of winter migrations and massive aggregations of target species in streams. Although, there was variation between species we were able to annually remove up to 35% of cyprinid fish species (individuals > 20 g) from Lake Søgård during our study. This was accomplished with a relatively limited working effort in terms of man-hours which suggests that reduction fishing from streams can be a cost-efficient supplement to traditional in-lake fish removal methods.

Hansson et al. (1998) suggest that cyprinid planktivore populations should be reduced by at least 50% in order for biomanipulations to result in detectable changes in the trophic structure of lakes, and although we approached this for white bream and roach in 2014 (35% and 27%), we did not fully achieve this suggested threshold. However, depending on species and study year up to more than 70%-80% of the cyprinids in our study lake aggregated outside the lake for shorter or longer periods during winter and could therefore, potentially, have been removed given maximum fishing success. This nicely illustrates the potential of this method and it is likely we could have reached a 50% removal, at least for some of the cyprinid species, with an increased or improved fishing effort, i.e. more fishing days and additional fishing gears. Interestingly, a species such as roach, which has been less effectively controlled by traditional biomanipulation measures (Søndergaard et al., 2008), was well targeted by the present method. However, the fact that some length classes and species were less prone to migrate, as compared to others, illustrates that the method cannot stand alone, but should be considered as a supplement to traditional in-lake fish removal methods.

Previous studies have highlighted that removal of bream and especially large, benthivorous bream is needed in order to obtain long term improvement of water clarity (e.g. Søndergaard et al., 2008). In Lake Søgård the large, benthivorous bream were less prone to migrate than smaller bream, and

similar patterns were seen for white bream. This size-specific variation could be explained by the fact that seasonal migration of cyprinids may relate to individual risk of predation (Brönmark et al. 2008; Skov et al., 2011; Hulthén et al., 2015), but as bream (and white bream) can outgrow the risk of predation by gape-size limited predators, their migration propensity also declines with increasing size (Skov et al., 2011). Therefore, in lakes where large bream should be removed, fishing needs to be combined with in-lake removal methods.

Roach also showed size-specific variation in migration propensity, but in the opposite direction compared to bream and white bream, i.e. small roach migrate less than larger roach. The mechanisms behind this could relate to size-specific trade-offs between growth and predation risks (Brönmark et al., 2008), which has been shown also in other lake systems (Brodersen et al., 2008a). Roach become more omnivorous and less zooplanktivorous as they grow (e.g. Horppila, 1994) and migration propensity increases with size in roach, hence we may have overestimated the amount of zooplanktivorous roach removed. Almost all large roach migrated and by repeating fishing effort for several years, i.e. more than two years as in this study, the likelihood of removing a large proportion of the larger roach and thereby a large spawning biomass is increased. Since large bodied individuals of roach could have a relatively higher reproductive output than smaller conspecifics, as shown for other species (e.g. Avery, 1985), we speculate that the reduction in reproduction in the following year may be even higher than the proportion of removed biomass suggest.

Removal of cyprinids is generally recommended to take place during winter, with the aim to reduce fish biomass shortly before a potential spring clear water phase (Perrow et al., 1997; Meijer et al., 1999; Gulati & Van Donk, 2002). However, as illustrated by this study, at this time not all target fish may be in the lake, which advocate for including stream fishing during winter as a supplementary method in the biomanipulation of shallow lakes. In line with this, we have direct or anecdotal knowledge of cyprinid fish aggregating outside lakes during winter season from several lakes in Sweden and Denmark (Jepsen & Berg, 2002; Borcherting et al., 2002; Brönmark et al., 2008; Skov et al. 2010; personal observations) and personal communications with fisheries ecologists throughout Europe suggests that it is common in other regions as well. Hence, we believe it is probable that seasonal migration is a common phenomenon. It should be noted, however, that the far majority of lakes from which cyprinid migration has been reported are shallow lakes (e.g.

Skov et al., 2008; Skov et al., 2010), and there are observations that suggest that seasonal migration is much less intensive in deeper lakes (Skov, unpublished).

As mentioned previously more than 70%-80% of the cyprinids > 20 g moved out of Lake Søgård during winter and therefore, at least in theory, could have been removed from the lake system, if fishing effort had been higher and more efficient. This illustrates the general potential of stream fishing as a biomanipulation tool although it should be recognized from this study as well as others (e.g. Skov et al., 2008; Brodersen et al., 2011) that the proportion of fish that aggregate in the streams may vary between years both within species and between species. In addition, it can vary substantially between different lake-stream systems even within the same year (e.g. Skov et al., 2010), highlighting that the mechanisms behind why and how many fish aggregate in the streams during winter is far from trivial. In line with this, previous studies have shown that a suite of different internal and external factors influence migration propensity and duration, including feeding conditions in the lake during summer and subsequent individual body condition (Brodersen et al., 2008a), fish size (Brodersen et al., 2008a; Skov et al., 2011), genetics and local adaptations (Skov et al., 2010), individual variation in boldness towards predators (Chapman et al., 2011), and perceived predation risk (Hulthén et al., 2015). Therefore, the magnitude of the migration may vary between lake systems and our experience is that it will require detailed lake specific knowledge to give lake specific predictions about how much biomass in theory can be removed. Still, the present study illustrates that the method can have great potential to supplement other methods.

From a management perspective, one of the strong advantages of this method is its cost-effectiveness. In the present fish removal experiment in Lake Søgård, each electrofishing session involved two people and took in total a maximum of 3 hours excluding transportation. In winter 2013/2014 this amounted to 90 man hours or 7.3 kg fish pr. man hour. In winter 2014/2015 only 18 man hours was used and, probably because we gained more experience with the method, the efficiency rose to 21.9 kg cyprinid fish pr. man-hour. Søndergaard et al. (2007b) gives some cost estimates of various biomanipulation methods based on Danish biomanipulation measures (Fig. 3). Here, the cheapest is fish removal (1750 Euro per ha lake area) and the most expensive chemical treatments, i.e. additions of aluminum to capture free P from the water phase (4450 Euro). A direct comparison between the present study and the numbers from Søndergaard et al. (2007b) is of course difficult and has to be interpreted with care. However, if we focus on our fishing effort in

2013/2014 (90 man hours), assume a price of 70 Euro per man hour and a cost to fishing equipment, e.g. electro fishing devices of 1400 Euro, then the cost pr. ha would be around 300 Euro, which compared to the numbers from Søndergaard is less than a fifth of the average costs for more traditional fish removal efforts in Denmark. Consequently, even if effort was doubled or tripled in order to increase the catch, the method would still be cost efficient.

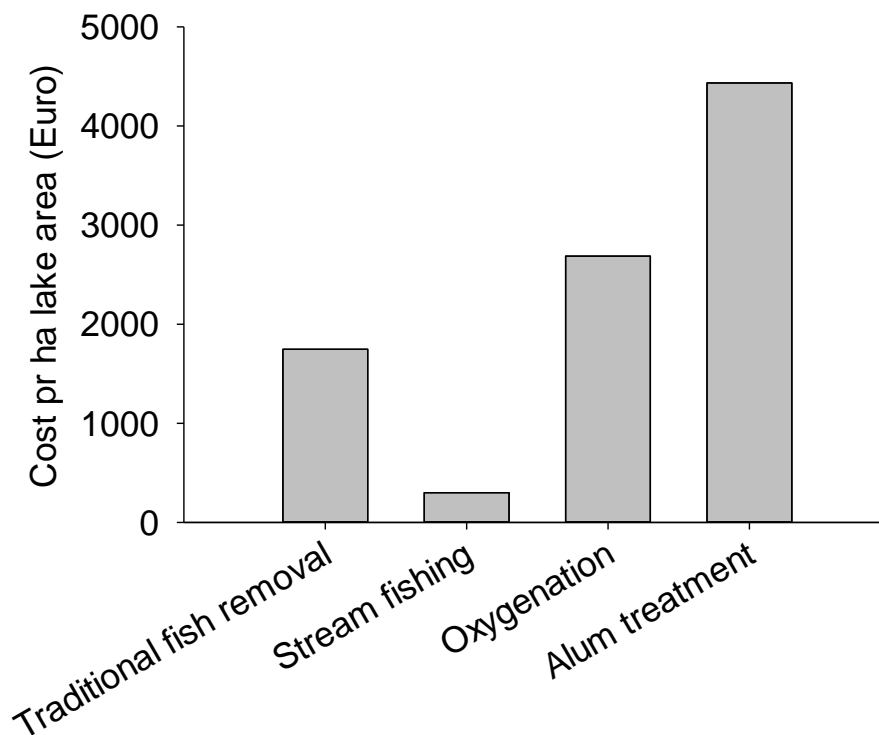


Figure 3: Comparison of the estimated costs associated with stream fishing in comparison with other lake restoration methods based on Danish experiences from Søndergaard et al., 2007b. We use the estimated costs from 2013/2014 where the number of man hours spend were highest, whereas data from Søndergaard et al., 2007b are average costs based on 17 traditional fish removal measures, 4 oxygenation measures and 4 alum treatment measures.

Based on the present as well as previous studies we are able to give some general recommendations to future lake managers about how to fish, where to fish, and when to fish for cyprinids in lake inlets and outlets during winter. That being said we can also see some ecological risks related to the present method that needs to be weighted in before implementing the method in future biomanipulation efforts.

How and where to fish.

In the present study, we used electrofishing as a method to remove cyprinids from the stream and it is likely that our efficiency could have been increased by using additional methods. Clearly, the

choice of fishing method will depend on local knowledge and in other systems different methods may be appropriate. Local knowledge is also needed in order to establish where the fishing should be conducted, i.e. where in the stream the cyprinids tend to aggregate as this will likely vary from system to system. Such knowledge of the exact whereabouts of fish in the stream could be obtained by walking along lake inlets and outlets during winter and visually inspect for the large schools of aggregated cyprinid fish easy to spot in the stream. Alternatively, knowledge about the exact whereabouts could be obtained by tagging a number of individuals with active telemetry tags, i.e. radio transmitters, in autumn prior to migration. By tracking tagged fish in the streams just before fishing sessions is conducted the potential positions of the aggregated fish could be elucidated and fishing efficiency improved. In lack of such data, an alternative could be to focus on fishing the slow flowing parts of the streams and channels as these are preferred areas by the cyprinids (Brodersen et al. 2008b; personal observations). Local knowledge is also needed to establish if winter migration mainly take place in the lake inlets, in the outlets or in both, as previous studies have shown that this can vary between lakes and within season (Skov et al., 2008; Skov et al., 2010, personal observations).

When to fish.

Knowledge about when fish migration peaks during winter will cost optimize fish removals from streams. Potentially, temperature could be a useful predictor of peak migration, as there seems to be correlations between water temperature and patterns of migration (e.g., Brönmark et al., 2008; Skov et al., 2010). In this study, most fish were observed in the inlet stream at temperatures below 6°C. Interestingly, in both seasons there was a return migration to the lake during mid-winter when the temperature dropped below 2°C. We speculate that this coincided with occurrence of ice cover on the lake as previous studies have indicated that ice cover can influence migratory behavior of cyprinid fishes (Heermann & Borchertding, 2006). Indeed, in 2013/2014 observations of ice cover on the lake supports this, as we observed ice cover on the lake on 28th January but not on 4th February. Unfortunately, we have no direct registration of ice cover occurrence and duration in 2014/2015 and water temperature measurements from the lake outlet may not be an accurate indicator for presence of ice. However, air temperature measurements from both study years obtained from Danish Meteorological Institute indicate that the potential for ice cover was indeed present slightly before and during the period of return migration, i.e. average air temperatures below 0°C (data not shown) were frequent. It is possible that fish could benefit from a return migration

during ice cover as predation risk in the lake could be reduced, e.g. because avian predation is prohibited or light conditions reduced leading to impaired foraging conditions for visually oriented predators. In summary, we tentatively suggest that fish removals are most efficiently done at water temperatures below 6°C but before ice cover establish on the lakes.

Evolutionary considerations.

Migratory populations will generally consist of obligate residents, facultative migrants, and obligate migrants in different proportions, some of which may be zero (Pulido, 2011; Brodersen et al., 2014). These proportions depend on the frequency distribution of migratory propensity, which can be seen as a liability trait, and the environment that determines migratory thresholds (Pulido, 2011). Some cyprinid species, like roach, generally increase the migratory rate with size (this study; Brodersen et al., 2008a) and very rarely change strategy once migratory (Brodersen et al., 2014), the proportion of migrants at larger sizes can give an indication about the occurrence and proportion of obligate residents in a population.

In our study system, close to all larger roach migrated, which suggest a low proportion or no obligate residents in the system. However, in other systems, this appears to be different. In Swedish Lake Krankesjön, a more deep bodied shape of larger non-migratory roach, resembling roach from fully resident populations (Chapman et al., 2015), the high condition of long term-residents (Brodersen et al., 2014) and the residence of about 20% of high condition large roach (Brodersen et al., 2008a), suggest a considerable amount of obligate resident roach in this lake.

We would expect that selective fishing on migratory fish in partially migratory populations would have evolutionary consequences on the relative frequency of obligate and facultative residents and migrants. Specifically, we would expect micro-evolutionary changes leading to a higher frequency of residents, especially when obligate residents are present. This would likely lead to a decrease in the proportion of migratory fish in the population and thereby also the possibility to effectively repeat fish removal in the streams. Since the proportion of winter migratory planktivores affect zooplankton average size over winter and subsequently timing of phyto- and zooplankton peaks in spring (Brodersen et al., 2011), which models suggest should affect the occurrence, timing and duration of clear-water phases in spring and thereby the (re)establishment of macrophytes (Brodersen et al., 2008c), increasing the proportion of resident fish may counteract the objective of the biomanipulation.

Finally, in other systems, selective fisheries have been shown to have the potential to induce evolution of life histories with consequences for population composition in freshwater fish, e.g. truncation of size and age distributions (e.g. Kokkonen et al., 2015; Olin et al., 2017) and decreased size and age at maturity (e.g. Matsumora et al. 2011; Kokkonen et al., 2015; Tiainen et al., 2017).

In conclusion, we recommend that these potential evolutionary costs are acknowledged and considered before engaging in reduction fishing endeavors in streams connected to lakes.

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Supplementary material

Supplementary table 1: The biomass removed (Remov.), number of recaptures (Recap.), average individual weight including 95% confidence intervals (Ind. W.), and number of individuals weighed (N) roach, white bream, and bream at each biomanipulation fishing event at the inlet stream of Lake Søgård in the 2013/2014 and 2014/2015 seasons (the table is illustrated on page 172).

Date	Roach				White bream				Bream			
	Remov. (kg)	Recap.	Ind. W. (g)	N	Remov. (kg)	Recap.	Ind. W. (g)	N	Remov. (kg)	Recap.	Ind. W. (g)	N
07-01-2014	9.5	2	62 ± 11	60	0.2	0	-	-	1.7	0	76 ± 18	30
14-01-2014	36.1	5	42 ± 7	60	5.1	0	58 ± 9	60	1.2	0	135 ± 39	9
20-01-2014	51.7	9	55 ± 10	60	2.9	2	58 ± 15	44	3.3	0	165 ± 28	20
28-01-2014	0.3	0	31 ± 5	20	0.0	0	-	-	0.0	0	-	-
04-02-2014	23.6	5	32 ± 3	57	1.5	0	40 ± 3	37	0.0	0	-	-
12-02-2014	64.6	9	40 ± 5	60	0.8	0	44 ± 5	19	1.5	0	101 ± 25	14
18-02-2014	100.2	8	39 ± 5	60	2.5	0	52 ± 14	53	2.1	0	92 ± 23	24
25-02-2014	43.5	9	38 ± 5	60	0.8	0	38 ± 4	22	0.2	0	-	-
03-03-2014	0.6	0	37 ± 10	18	0.0	0	-	-	0.0	0	-	-
12-03-2014	32.4	5	47 ± 9	60	0.0	0	-	-	0.0	0	-	-
17-03-2014	71.4	9	43 ± 6	60	13.3	1	120 ± 9	122	27.6	8	126 ± 15	60
25-03-2014	51.8	6	53 ± 8	60	5.1	3	76 ± 9	160	4.2	0	122 ± 18	35
01-04-2014	40.6	5	36 ± 4	60	9.9	2	49 ± 5	156	0.3	0	-	-
08-04-2014	22.9	4	38 ± 4	60	2.9	1	62 ± 8	180	0.2	0	-	-
14-04-2014	17.5	5	35 ± 4	60	5.1	3	47 ± 4	60	0.5	1	48 ± 43	5
15-02-2015	151.3	11	51 ± 11	66	8.3	1	128 ± 33	65	7.3	0	190 ± 71	28
04-03-2015	109.4	11	34 ± 3	79	3.8	1	56 ± 13	68	3.9	1	88 ± 34	44
18-03-2015	99.4	14	45 ± 4	89	4.3	0	91 ± 26	47	4.4	2	145 ± 65	26

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